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DIE ERNÄHRUNGSÖKOLOGISCHEN BEZIEHUNGEN ZWISCHEN *ASIO OTUS OTUS* L. UND IHREN BEUTETIEREN, INBESONDERE DEN MICROTUS-ARTEN
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ECOLOGICAL MONOGRAPHS

VOL. III JULY, 1933 No. 3

ALPINE PLANT SUCCESSION ON JAMES PEAK, COLORADO

(With Twelve Figures)

By

CLARE FRANCIS COX

Indianapolis, Indiana

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY, UNIVERSITY OF CHICAGO.

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ALPINE PLANT SUCCESSION ON JAMES PEAK, COLORADO[1]

INTRODUCTION

Comparatively little has been done on this continent in the investigation of environmental conditions and plant succession in the alpine zone of the high mountains and in the arctic region. Data concerning conditions affecting plant life in these regions are extremely limited. The present work is the result of a fairly intensive study made of a small area in the alpine zone. In addition to methods commonly applied in the investigation of the vegetation by American ecologists, the writer has used the statistical method as employed by European investigators in their study of the plant associations in the Alps and in northern Europe.

The summers of 1928 and 1929 were devoted to the work in the field, practically the entire vegetative season being spent within the alpine zone. Limitations as to time and facilities available for carrying on field work in the mountains far above all settlements in a region where severe storms frequently interrupt the short growing season made it impossible to carry on detailed study of all the important factors. Quantitative measurements were made of altitude, exposure, temperature, length of growing season, evaporation, and soil acidity. General observations only were made of the effect upon the plants of the climatic factors, light, rainfall, wind, and soil. Attention was also directed towards the effect of the biotic factors, grazing, fires, and lumbering. The statistical method of Raunkiaer with certain modifications was used to determine the floristic composition of the plant associations and to trace the origin, development, and decline of these units of vegetation. Considerable attention was given to the presence in a given community of certain plant species of well defined life requirements as indicators of ecological conditions in the habitat. Such species may sometimes serve to a certain extent as a check on the data obtained by instruments or upon conclusions reached by a more or less superficial study of a habitat. A passive inorganic instrument does not always measure the effect of a particular stimulus upon living protoplasm.

Grateful acknowledgment is hereby made to Professor George D. Fuller of the Department of Botany, University of Chicago, for advice and criticism throughout the present study; to Aven Nelson, A. S. Hitchcock, C. R. Ball, C. C. Plitt, Theodore Holm, and Kenneth K. Mackenzie for their liberal and valued assistance in the determination of the plants; to my wife, Lissa, for help in the collection and preservation of the plants and for assistance in making the plant population studies upon which the work is so largely based; and

[1] A contribution from the Hull Botanical Laboratory, University of Chicago.

to Mr. and Mrs. Oliver W. Toll of Denver, Colorado, whose generous hospitality facilitated the carrying out of the investigation. The writer furthermore welcomes this opportunity to express his gratitude for the assistance afforded in carrying on this work by the John Merle Coulter Research Fellowship in Botany.

GEOLOGIC HISTORY

The area to which this study has mainly been confined comprises some ten or twelve square miles extending eastward from James and Parry Peaks, (Fig. 1) which lie along the crest of the Continental Divide, to the site of the

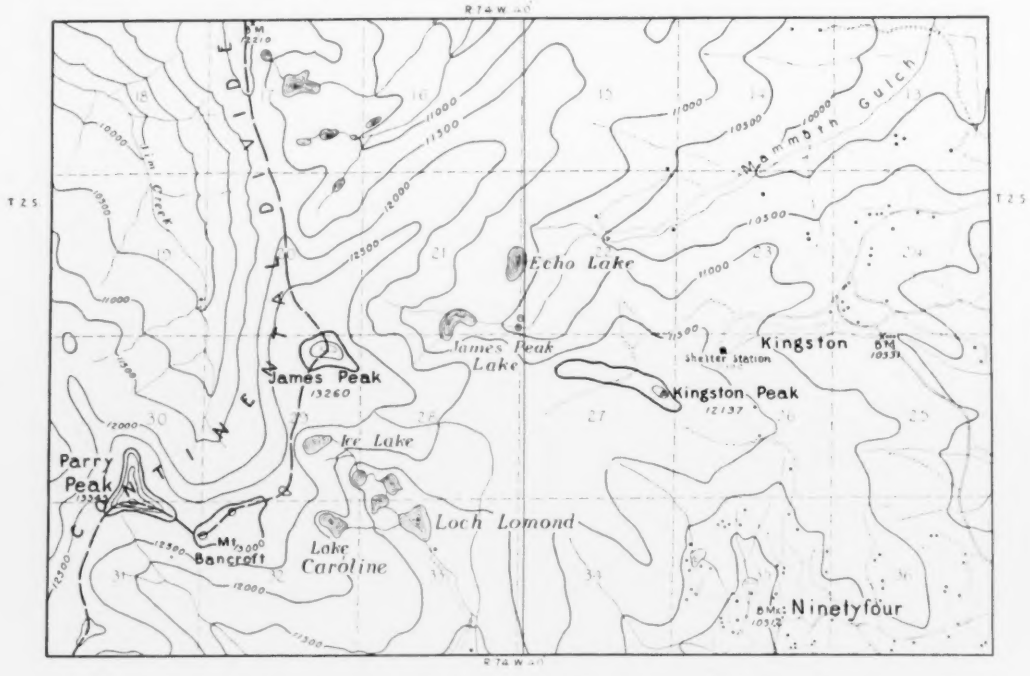

FIG. 1. Map of James Peak, Colorado. The area under investigation extends from James and Parry Peaks on the Continental Divide eastward to Kingston village. (U. S. Geol. Surv. Colo. Central City Quadrangle, modified by omission of all but 500-foot contours except on Kingston Peak above 12,000 feet and on James, Parry, and Bancroft Peaks above 13,000 feet where 100-foot contours are retained.)

former village of Kingston. James Peak is about forty miles almost straight west of Denver. The region lies within the area marked on geological maps of Colorado as Pre-Cambrian which is described by George (1927) as being a complex of granites, gneisses, and schists rendered extraordinarily complex by intrusions of granite and other igneous rocks. Sedimentary deposits of Pre-Cambrian or later eras, as well as these igneous intrusions, have either been removed by erosion or have been so completely metamorphosed as to have lost their original structure. Limestone does not occur within the area.

The scanty soil which sometimes overspreads the gentler slopes and valleys or is lodged among the rocks has resulted from the weathering of the

crystalline rocks and from the decay of plant remains. Much of the area is a broad upland, a large part of it possessing a comparatively gentle relief for mountain territory of such great elevation, and showing little or no sign of glacial action. But two great cirques, one at the head of Mammoth Gulch to the northeast of James Peak, containing Echo and James Peak Lakes, and one to the south, containing Loch Lomond and Ice Lake (Fig. 2), constitute evidence of ice erosion during Pleistocene times. All these lakes owe their existence to the work of mountain glaciers, the heads of which were at the upper end of the valleys some distance above timberline. The uplifting of this region to its present elevation took place mainly in the late Tertiary Period (Blackwelder and Barrows 1911), and subsequent erosion is responsible for the present relief. The altitude varies between 10,500 and 13,345 feet, but the greater part of the vegetation dealt with in the present study occurs on the mountain slopes between 11,000 and 13,000 feet.

FIG. 2. Alpine expanse looking southwestward from Kingston Peak towards Continental Divide. James Peak and glacial cirque at head of Mammoth Gulch at right; Parry Peak in left center and Mt. Bancroft at extreme left. Large gulch between James Peak and Mt. Bancroft heading against Continental Divide. Photographed July 1, 1931.

PHYSIOGRAPHY

Outstanding in alpine altitudes, at least until later stages of the erosion cycle are reached, is the barrenness resulting from the great amount of exposed rock. Due to vigorous action of wind, water, and ice, soil is not permitted to accumulate over much of the region even though soil forming forces may be active. Great boulder fields commonly occur on top of massive

summits such as are characteristic of James and many other peaks of the Colorado Rockies. Boulder fields are also frequently encountered on rounded ridges, on mountain flanks of moderate relief, and at the foot of precipitous slopes and cliffs. Slides or talus slopes of unstable rock fragments extend upward from the bases of steep slopes and precipices. In cracks and crevices of the rocks and on flat ledges and surfaces of moderate relief the smaller particles of rocks waste are first permitted to accumulate, and it is in such places that the first vascular plants gain foothold. Since there are many species of plants that can withstand the rigors of the alpine climate on James Peak, the great barrenness of much of the region is due to activity of erosion, to lack of soil, and to late lying snow which in many places reduces the growing season too much to permit plants to complete their life cycle.

Two deep gulches were carved out of the rock by the Pleistocene ice. The upper ends of these glacial valleys for a short distance lie within the area under investigation. Sufficient time has not elapsed since these valley floors were swept clean by the ice for the present streams to entrench themselves in the hard rock. Only a comparatively thin covering of soil has been formed and in many places it is coarse in texture and contains little humus. The greatest soil-accumulations occur in marshy areas about streams and lake margins and at the foot of many of the slopes around the valley, especially at the lower edge of snow drifts in places favorable for the development of vegetation.

Upon the upper mountain slopes in places of moderate relief, the mantle rock has perhaps been less disturbed for a much longer period except on surfaces exposed to wind. Few of the streams on these slopes are of any size, and only three or four of them flow continuously throughout the season. During early summer while the snow is melting and during late summer for a few hours following heavy showers, they are active carrying rock waste down the slopes; but due to the hardness of the underlying rock they have nowhere cut any deep channels. Here, as in the glaciated valleys below, the most extensive soil deposits occur about springs and seepage areas and along streamsides where soil formation is favored.

CLIMATIC FACTORS

Temperature.—The limited data available concerning winter temperatures in the higher Rockies come from records kept for a few years on Pike's Peak, at Corona, which is on the Continental Divide a few miles north of James Peak at 11,660 feet, and from occasional reports from isolated points in the mountains. The records kept at Corona (Dodds 1917) indicate a mean annual temperature of 26°F. for that altitude and show that frosts may occur almost any week during the summer. The 26° isotherm on a temperature map of the world passes through Alaska, Labrador, and Greenland. This indicates for the high alpine region a climate approaching closely

that of the arctic. However, it seems certain that much lower temperatures are reached in Montana and various parts of Canada at moderate altitudes where forests are well developed than in the alpine regions of Colorado. Studies made in the Alps (Brockmann-Jerosch 1919) on the relation of low temperature to the occurrence of tree vegetation indicate that length of growing season and exposure to desiccating effect of winds during periods when the ground is frozen are more critical than winter temperatures in determining the tree limit in the alpine zone and in the far North.

The thin atmosphere at these high altitudes has little capacity for retaining heat and it changes temperature rapidly after the sun disappears. Heat is quickly radiated from rocks and soil at night. A wide range in daily temperature is noticeable during the summer months. Low temperatures during the alpine growing season are decisive in their effect on the vegetation. Late frosts may destroy new growth in late spring or summer; and where the growing season is so brief, it will not permit a second growth to reach maturity. Great contrasts occur between sun and shade temperatures and between south and north exposures. This is very noticeable in the difference in time of flowering of species occurring in both locations.

During the summers of 1928 and 1929 complete records were kept of daily maximum and minimum temperatures at a station at the lower edge of the alpine zone at 11,300 feet (Table I). The thermometers were placed on the northwest side of a building where they were sheltered from the direct rays of the sun at a height of four feet above the ground. The record maintained at this station from June 28 to August 27, 1928 and from June 21 to August 26, 1929 covers practically the entire growing period in the alpine zone and shows temperatures of 32° F. or lower in 1928 on June 28, July 1, 8, 25, August 3, 4, 23, 24, 26, and 27. The record for this same period during 1929 kept at the same station with the same thermometers failed to show a single freezing temperature although the record for this second summer shows temperatures of 40° or lower on 22 different days. The maximum temperatures were practically the same during 1928 and 1929, averaging 65° both summers and reaching 70° or above, 15 times in the former year and 13 times in the latter. The minimum temperatures averaged 39° in 1928 and 41° in 1929. The mean daily temperature for these two seasons is therefore seen to be practically the same in spite of a considerable number of days with greater extremes in the summer of 1928.

The explanation of the differences in the two summers is relatively simple when one knows all the weather conditions during the two seasons. The summer of 1928 was, with the exception of a three week period, a dry summer with much bright sunny weather and relatively few cloudy, rainy days. The summer of 1929, on the other hand, with the exception of about three weeks, was almost continuously wet with most of the days cloudy or rainy. The cloudy condition and humid atmosphere in 1929 served to equalize the ex-

TABLE I—*Daily summer temperature record*

Date	1928		1929		Date	1928 (Cont.)		1929 (Cont.)	
	Max.	Min.	Max.	Min.		Max.	Min.	Max.	Min.
June					July (Cont.)				
21	..	..	66	36	25	58	32	70	42
22	..	..	64	35	26	66	40	74	45
23	..	..	58	40	27	60	42	64	45
24	..	..	58	34	28	64	39	59	35
25	..	..	64	35	29	66	40	62	43
26	..	..	65	46	30	64	46	63	42
27	..	..	70	42	31	70	45	60	43
28	64	32	74	40	August				
29	72	36	72	42	1	64	47	62	46
30	66	33	68	44	2	60	40	66	46
July					3	57	32	56	44
1	70	32	67	37	4	56	32	62	44
2	68	33	68	35	5	59	37	58	45
3	70	42	65	38	6	62	34	53	40
4	72	41	66	40	7	61	39	62	36
5	64	44	70	35	8	68	34	62	40
6	70	44	68	39	9	70	37	58	36
7	64	36	65	40	10	66	38	60	40
8	66	31	70	36	11	68	40	64	40
9	72	42	65	38	12	68	45	64	36
10	78	38	65	40	13	67	42	66	35
11	74	38	66	39	14	70	42	68	40
12	72	37	67	43	15	63	44	70	46
13	70	40	68	39	16	61	42	73	47
14	66	44	67	43	17	67	36	66	43
15	68	38	72	38	18	70	46	64	38
16	66	45	76	44	19	64	36	66	44
17	59	40	70	44	20	65	46	65	42
18	68	42	66	40	21	70	42	62	45
19	64	42	69	43	22	66	48	64	41
20	65	42	66	47	23	53	28	62	38
21	62	40	69	43	24	60	29	64	43
22	63	39	70	42	25	56	42	60	42
23	56	38	65	45	26	54	30	64	42
24	53	36	64	41	27	56	27	..	..

	1928	1929
Mean Daily Temperature	52	53
Mean Maximum Temperature	65	65
Mean Minimum Temperature	39	41
Mean Daily Temperature Variation	26	24

treme temperatures of bright warm days and clear frosty nights such as occurred in 1928.

Soil temperatures at the surface of the ground may be considerably different from air temperatures four feet above the ground. Differences in sun and shade temperatures are considerable at the same distance above the surface. A few soil temperatures taken at the surface of the ground on a south sunny exposure at the station showed a temperature as high as 90° at 11:00 A. M., when the thermometer in the station registered 70°. Ice was formed on a small mountain rill near by on nights when the thermometer at the station registered no lower than 37°. A daily temperature range of

40° F. was obtained there; but the ranges at the soil surface at this altitude were noticed in a few instances to be as great as 60° F. in a 24 hour period. Consequently, the temperature record as kept gives only a limited idea as to the extremes which occur in the alpine zone.

The significance of the temperature factor in its effect upon alpine vegetation can best be appreciated when one considers the low daily minimum and the frequency with which the temperature reaches or approximates the freezing point during the brief growing season. The maximum temperature often comes between 10:00 and 11:00 A. M. Frequently the wind arises or clouds form about this time, and the temperature soon falls. On very few days does high temperature last long. It is always cool by sunset and remains cold all night. Such conditions must be effective in dwarfing and in otherwise determining the characteristics of the plants of the region.

The data collected are sufficient to show that in much of the alpine zone at least freezing temperatures may be reached at any week during the growing season. The alpine growing season then cannot be measured in frostless days as is frequently the practice in lower altitudes. The vegetation must consist of plants which can survive in spite of these extreme temperatures. Along the bottoms of valleys, especially in deep canyons, cold air may flow down for considerable distances, the late freezes destroying species which are able to survive on the higher slopes. Late lying snows may accumulate in such places and prevent the plants of lower altitudes from occupying them. Alpine species frequently occur in such places at lower altitudes than on the higher valley sides where subalpine vegetation may prevail. Tree vegetation is frequently absent from the valley floors while alpine meadows border the streams and extend down into what appears, from the forests on the valley slopes, to be subalpine zone. Alpine growing conditions may thus be extended to lower altitudes.

Light.—Light varies more perhaps in different parts of the alpine zone than at lower altitudes. This is made possible because of the high altitude, the thin transparent atmosphere, and the areas of snow with high reflective capacity. A large proportion of the light received by alpine vegetation i direct, and a smaller proportion is diffuse than is the case with vegetatio of lowlands. Frequent cloudiness, however, reduces the total light received and converts a large proportion of direct to diffuse light.

Several theories have been advanced concerning the effect of the intense light upon the plants. Intense light is known to be destructive to chlorophyll. Henrici (1918-19) found that leaves of alpine species contain less chlorophyll than the same species from lower zones. Schanz (1918, 1918, 1919) thinks the ultra-violet light waves are responsible for the dwarfed condition of the plants, the brilliant colors of the flowers, and the thicker leaves with increased palisade tissue and lignification.

Since different species have different light requirements, the matter of

distribution into communities is influenced by the light factor. Plants growing on steep north slopes, in deep narrow valleys, in the shadows of boulders, and in lower layers of several-layered communities, such as the wind timber, commonly have thinner leaves with more chlorophyll than do plants growing in open meadows or other places exposed to the sun; e. g.: *Viola biflora, Saxifraga caespitosa, Adoxa moschatellina.* Species of extremely low light requirements, such as certain lichens, mosses, and flowering plants which may come almost into flower before the snow is completely removed, are frequently to be found where snow lies until late summer. Plants with leaves covered with hairs or sometimes with scales are characteristic of exposed situations; e.g.: *Eritrichium argenteum, Actinea lanata, Trifolium dasyphyllum, Artemisia pattersoni.* Plants of exposed habitats are pronouncedly xeromorphic. Those subject to the desiccating action of both sun and wind are most decidedly so. Fell fields on southwest exposures are sometimes almost devoid of vegetation except in cracks and crevices which afford shelter against sun and wind.

Precipitation.—The major portion of the precipitation in the alpine zone is in the form of snow and occurs while vegetation is inactive. The rain comes commonly during the summer months in showers of brief duration occurring about noon. Data concerning the annual precipitation in alpine altitudes in the Rockies are extremely limited. The weather station maintained for several years on the Continental Divide a few miles north of James Peak recorded a total precipitation of 43.69 inches (Dodds 1917). The snowfall amounted to 390.6 inches (32.5 feet). Snows may occur during any month but come mostly from September to May. The rain occurs in June, July, and August. Sleet and hail are not infrequent during July and August. Records kept on Pike's Peak (Whitfield 1933) at montane, subalpine, low alpine, and high alpine stations show a gradually increasing precipitation with increasing altitude up to the lower alpine zone and a decreased precipitation above. This is in accord with records kept in the Alps.

In the present investigation the data concerning rainfall are limited to rather detailed daily observations concerning showers, state of the atmosphere with reference to clouds, mists, and wind. In case of rain, the time, duration, and intensity of the precipitation were noted. Such a record made it possible afterwards, when interpreting the quantitative data obtained in the evaporation studies, to determine the kind of weather at any time during the summer.

Table II summarizes some of the observations on precipitation, humidity, wind and light factors during the course of the investigation recorded in number of days. Under such a relative scheme it is, of course, difficult or impossible to classify some of the days; hence the totals in some cases may fail to account for the full number of days. The value afforded by such a scheme can best be appreciated when it comes to interpreting fluctuations

TABLE II—*General observations on rainfall, wind, and humidity*

	1928 June 24—August 27		1929 June 21—August 26	
Length of period	65 days		67 days	
Rain, heavy or prolonged	14 "	20	26 "	44
Rain, light	6 "		18 "	
Rainless	43 "		23 "	
Wind, brisk to strong	33 "		18 "	
Wind, moderate	28 "		31 "	
Calm (little or no wind)	4 "		15 "	
Bright, sunny most of day	32 "		12 "	
Cloudy, much of day	17 "		49 "	

in evaporation rates with respect to the possible part played by humidity, light, and wind in this process.

A study of the complete data kept indicates that in 1928 clear weather with moderate to brisk winds almost daily and only two or three light showers prevailed from June 24 to July 15. Then followed three weeks, July 15 to August 7, during which there were on an average two or three heavy showers each week and one or two light ones. There were only two or three bright days without rain each week. From August 7 to 27 the weather was fair again with only four heavy showers during the three weeks. In contrast with the 1928 season, that of 1929 started with a clear rainless period which lasted from June 20 to June 30. The stormy period then set in, lasting until August 6 with only about two rainless days each week and some weeks none. Storms frequently began by 10:30 to 11:30 and lasted late into the day, and occasionally into the night. August 7 to 15 was a period of bright, sunny, rainless days. The rest of the season, from August 15 to 26, was characterized by stormy weather with almost daily showers which were frequently of long duration.

The precipitation occurring during winter in the form of snow is of great importance to alpine vegetation. Snow acts as a reservoir for a considerable part of the water used by the plants during the growing season. Melting occurs so late and so gradually that the percentage of loss from run-off is less than would occur in case of the same amount of precipitation on the mountain slopes in the form of rain.

During bright rainless periods of early summer, water from melting snow maintains favorable growing conditions on many slopes. In years of little winter snowfall such periods are sometimes critical for certain species. In the Alps and in the Canadian Rockies a large perpetual snow cap furnishes water and more favorable conditions of humidity for the vegetation all summer.

While snow fields tending to assume the conditions of small glaciers are found on some of the higher peaks of northern Colorado, there is nothing

more extensive than large snowdrifts on James Peak. In sheltered places some of these frequently last throughout the summer. The size of the drifts and the time of their disappearance from most of the upland slopes vary considerably from year to year, indicating a considerable difference in the amount of snow in different years. In 1928 on July 12 there was considerable snow at elevations from 11,000 to 12,000 feet even on slopes exposed to the sun. In 1929 by July 1 most of the snow had disappeared. In sheltered places among the trees in the subalpine zone snow may frequently be found after it has disappeared from most of the alpine slopes.

Snow in the alpine region is of great importance aside from its value as a source of water supply. The whole matter of distribution of species and communities is intimately connected with the presence or absence of a winter snow-cover and with the time at which the snow disappears in summer. Due to the constancy of direction of the prevailing winds, the snow accumulates in the same places year after year and is blown off others leaving them exposed. Certain species, as *Erigeron melanocephalus*, require the protection of this cover; some, like *Arenaria sajanensis*, appear to be indifferent to it; still others, like *Trifolium nanum*, occur only on areas kept practically free from snow or in places from which snow disappears at an early date. The peculiar habit of growth of the wind timber is caused in part by its winter snow cover which weighs the trees down. The depth of the snow determines their height. Species like *Sibbaldia procumbens* and *Erigeron melanocephalus*, requiring snow protection and consequently associated in spots where snow lies late, give rise to the well known snow flush communities. Oswald Heer (1836) first called attention to such spots, applying the classic name "Schneetälchen" (snowflush). Some species characteristic of windswept fell fields are rarely found where snow accumulates and are sometimes referred to as snow avoiding plants. Zonation of the vegetation is frequently brought about by variations from no snow cover to deep covering of late-lying snow.

During 1928 there was considerable evidence that vegetation suffered during the periods of bright rainless days and brisk winds. Particularly on rocky slopes, with little soil, exposed to both wind and sun, certain species of plants in places where soil water was insufficient to replace the rapid transpiration loss appeared to dry up without maturing seed.

Growing season.—Alpine growing season varies with latitude, altitude, exposure, and duration of snow cover. The growing season for areas kept free from snow is best considered as the period during which most of the frost is out of the ground. For areas where snow accumulates, it is the number of days without snow cover. Data submitted in the discussion of temperature and snow fix this period as varying from about three and one one half months in the most favorable spots to a few days or no period at

all where snowdrifts last all summer. For most of the region it amounts to from six to ten weeks.

Since frost may occur during almost any week of the summer, alpine vegetation is limited to species able to withstand freezing temperatures during their vegetative activity, to complete the life cycle from bud to seed in a few weeks, and to persist by vegetative propagation during years when seed fails to mature. The brief growing season excludes annuals and ranks first among factors determining the species which can succeed in the alpine zone.

Exposure, altitude, and slope.—Exposure and slope are important in relation to light, wind, temperature, evaporation, and soil moisture in any region of noticeable relief. Differences in altitude can be neglected except on mountains. In high mountains the effect of great relief upon most climatic factors appears to be to intensify them somewhat in proportion to the relief of the region. This explains the wide variations in amount of soil and snow accumulations, in time of melting of snow, in time of blooming of a given species, and in the species and plant associations at stations in close proximity in the alpine zone. Habitats, species, and associations embraced in a few square miles may be as varied as in a lowland region extending over many degrees of latitude and longitude. The great diversity results from the wide range of intensities of the climatic factors made possible by extreme differences of exposure, altitude, and slope.

An aneroid barometer and a pocket compass were always carried for determining altitude and exposure. The slope was estimated as nearly as possible without special equipment. Data obtained are recorded and their significance is discussed in the sections dealing with the various climatic factors.

Wind.—Wind affects vegetation mechanically by its pressure and physiologically by increasing evaporation. The former action brings about transportation of pollen and seeds and causes deformation of the plant as a result of injury to growing points. The abrasive action of sand and snow and the distribution of snow and soil also represent this type of wind action. Constancy of direction of prevailing winds causes accumulation of snow in certain places year after year and exposure of others. Flat tops of patches of wind timber indicate the average depth of winter snow. Clumps of dead wind timber point to insufficient snow cover, possibly in combination with late freezing. The killing of branches or trees, in so far as it results from the desiccating action of the wind in increasing transpiration, illustrates the physiological effect of the wind upon vegetation. Spaces free from limbs on tree trunks just above snow level indicate that abrasive action is greatest at the surface over which the wind blows.

In windswept areas where vegetation has succeeded in developing a continuous sod, the surface may become broken in certain spots, and the strong wind may gradually extend the openings until basin-like depressions are laid

bare. (Fig. 10). In such places vegetation can regain foothold with great difficulty and only after a long period.

The upper limit of tree growth on mountains has been found to be determined not so much by low temperature as by the physiological effect of wind in increasing transpiration. Other contributing causes are not to be overlooked. The subject of alpine timberlines has been discussed in detail by Shaw (1909) and by Brockmann-Jerosch (1919) who give extensive bibliographies dealing with this topic.

Species possessing great resistance to wind injury characterize the vegetation of wind exposed areas of the alpine zone. Cushion and mat forms and the rosette habit so common on fell and boulder fields are types of growth adjusted to steady and long continued action of the wind such as occurs at high altitudes (Fig. 4). Certain plant associations are characteristic of wind swept ridges and mountain slopes. Extensive study has been made of this type of vegetation in Lapland by Fries (1913). On James Peak various lichens, *Trifolium nanum*, *Paronychia pulvinata*, *Arenaria sajanensis*, *Phlox caespitosa*, and *Dryas octopetala* frequently dominate plant communities in the wind-swept areas.

Zonation of the vegetation is conspicuous and definite where different degrees of exposure to wind are encountered in places in close proximity as on windward and leeward sides of a mountain ridge or of large boulders. Very different vegetation types occupy windward and leeward slopes. Cold air drainage in lower alpine altitudes frequently extends alpine conditions and vegetation lower along deep ravines and valley floors than on their sides.

In the present study only such information concerning wind velocity was secured as could be obtained from general daily observations, from the apparent wind effects on the vegetation in different exposures and altitudes, from the positions and amounts of snow accumulations, from evidences of wind erosion and deposition on different slopes, and from comparative rates of evaporation in different altitudes and exposures. General daily observations concerning wind are summarized in Table II.

Evaporation.—Evaporation is not an exact measure of the loss of water from plants. Devices for measuring evaporation can not take into account the modified rate resulting from stomatal control, from differences in density of cell sap in different species, or from possible changes in the permeability of plant membranes. Since the evaporation rate gives valuable information concerning transpiration and water relations of the plant, especially when considered in connection with precipitation, it is commonly determined as a means of gaining knowledge concerning the water economy of the plant community. Factors commonly recognized as affecting the evaporation rate are wind, temperature, humidity, and radiant energy.

Atmometers were operated in pairs at a number of stations at different altitudes and exposures in alpine and subalpine zones during the summers

of 1928 and 1929. Livingston porous spherical atmometers were used; the methods employed were those which have come to be practically standard for these instruments. More time was devoted to evaporation study in 1928 than in 1929. The object in 1928 was to get information concerning the relation between evaporation rates at different altitudes and at stations of different degrees of exposure to wind and sun. During 1929 the object was, in addition to making a comparison of evaporation rates during the two seasons at some of these same stations, to determine any differences which might exist in evaporation rates of places with plant populations showing different floristic composition; that is, rates in different plant associations irrespective of differences of altitude and exposure.

Strong contrast in the weather of the two summers was indicated by data on rainfall, light, wind, and temperature. This was emphasized by differences in evaporation data which show the integrated effect of these factors upon evaporation rate.

A study of Table III which summarizes the average daily evaporation

TABLE III—*Average daily evaporation rates at alpine and subalpine stations*

Stations	Slope	Exp.	Altitude	Daily evaporation rate in cc.	
				1928	1929
Sedge-grass meadow	10°	NW	10,500 ft. subalpine	32.6 Aug. 1–26	
Spruce-fir forest	8°	E	10,700 ft. subalpine	13.2 July 9-Aug. 26	
Wind timber (sheltered)	8°	E	11,250 ft. transition	13.7 July 9-Aug. 26	7.0 July 12 - Aug. 26
Mesophytic meadow	10°	E	11,300 ft. alpine	31.0 July 9-Aug. 24	20.0 July 12 - Aug. 26
Dryas slope (exposed)	15°	E	11,300 ft. alpine	....	24.0 July 12 - Aug. 26
Wet meadow	5°	E	11,500 ft. alpine	....	17.0 July 12 - Aug. 26
Dry meadow (exposed)	15°	SE	11,500 ft. alpine	36.7 July 10-Aug. 26	24.3 July 12 - Aug. 25
Climax meadow: Elynetum	15°	NW	11,500 ft. alpine	....	23.3 July 14 - Aug. 25
Fell field (exposed)	20°	NW	11,900 ft. alpine	43.2 July 15-Aug. 26	24.5 July 12 - Aug. 25
Fell field (exposed)	20°	SW	12,000 ft. alpine	46.5 July 10-Aug. 26	
Boulder field meadow transition	20°	NW	13,200 ft. alpine	23.8 July 15-Aug. 14	

rates for the two seasons at the different stations shows the highest rate on rather barren fell fields of the lower alpine zone, next highest on the open grassland of alpine meadow, and a very much lower rate in the forest vegetation of the subalpine zone below.

In general, the results obtained point to an increase in evaporation rate with increase in altitude and in degree of exposure to wind and sun to about mid-alpine altitude. Since but one station was maintained at high alpine and this for only thirty days, the evidence is probably insufficient to justify the conclusion that evaporation rates are less here, although the results obtained during the time this station was operated indicate such a relation. Since rainfall has been found to be less at high alpine levels (Whitfield 1933),

TABLE IV—*Comparison of daily evaporation rates at different stations during the rainy week of July 24-31, 1928 and the dry week of August 17-24, 1928*

Station	Slope	Exposure	Altitude	Daily evaporation rate	
				July 24-31	August 17-24
Spruce fir forest.....	8°	E	10,700 ft. subalpine	9.0 cc	18.6 cc
Wind timber (sheltered)..	8°	E	11,250 ft. transition	4.8 cc	17.1 cc
Dry meadow (exposed)...	15°	E	11,500 ft. alpine	21.9 cc	52.9 cc
Fell field (exposed).....	20°	NW	11,900 ft. alpine	27.3 cc	54.0 cc
Fell field (exposed).....	20°	SW	12,000 ft. alpine	26.8 cc	58.3 cc
Mesophytic meadow.....	10°	SE	11,300 ft. alpine	15.0 cc	44.6 cc

one is tempted to conclude that the condition responsible for the decrease in precipitation, which is probably lower vapor holding power of the air at this altitude, would result in a lower evaporation rate here than at somewhat lower elevations. Frequent clouds or mists about high mountain peaks when it is clear below suggest that the air is often more nearly saturated at this high altitude than at lower altitudes. At this high alpine station near the summit of James Peak at 13,200 feet on a northwest exposure, a mesophytic meadow appeared to be developing. This points to high humidity or to high soil-water relation. The latter might result from decreased evaporation. Exposure to sun was slight at this station, but no more so than at a station maintained at 11,900 feet which showed a much higher evaporation rate. Possibly the evaporation rate at the higher alpine station would have been greater had the station been operated throughout the month of August. As might be expected, stations located in the same vegetation type, e.g. wet and

dry meadows, but in positions of different exposure show considerable difference in evaporation rates even at the same altitude. Floristic composition varies as much at these points as does evaporation rate.

Table IV shows the daily evaporation for a week of rather consistently cloudy, rainy weather from July 24 to 31, 1928 and for a week of as consistently clear, windy, rainless days from August 17 to 24 during the same summer. The limited data available for the higher altitudes of the Colorado Rockies indicates that weather of such a character is typical of the alpine summer. Late July or early August frequently constitutes a wet season of from one to three weeks being preceded and succeeded by periods of clear weather with little precipitation. A comparison of the average daily evaporation rate for July 24 to 31, 1928 with the daily rate for the whole observed season of 1929 at three stations operated at identical points during the two summers and a similar comparison of the evaporation at these stations for August 17 to 24 with the rates for the whole season of 1928 is impressive. These comparisons show a rather convincing correlation between the inte-

TABLE V—*Average daily evaporation rate of different vegetation types*

Vegetation type	Locality	Investigators	Evaporation in cc.
Beech-maple forest	Indiana	Fuller (1914)	7.0
Beech-maple forest	Indiana	Cain and Friesner (1929)	6.6
Pine dune forest	Indiana	Fuller (1914)	10.4
Western climax forest	Washington	Weaver (1914)	8.4
Alpine scrub forest	Colorado	Cox	10.0
Edaphic prairie grassland	Illinois	Fuller (1914)	12.5
Western prairie grassland	Nebraska	Weaver (1914)	20-30
Alpine mesophytic grassland	Colorado	Cox	25.5
Alpine climax grassland	Colorado	Cox	30.5
Alpine fell field desert	Colorado	Cox	43.2

grated action of wind, sunlight, and humidity and the rate at which evaporation proceeds. Data obtained from the other stations during these two particular weeks and during the entire season of either 1928 or 1929 are also consistent in indicating such a relation.

A comparison of evaporation rates in alpine plant communities with rates in lowland communities should throw some light on the differences of the vegetation of the regions. Table V gives results obtained by investigations in several communities in different regions.

While Table V gives merely average evaporation rates in the various vegetation types and not the extremes which doubtless are decisive in the case of evaporation as for other factors, it seems to point to a general trend towards increased xerophytism expressed in the vegetation of a region as one goes from a region of lower to one of higher evaporation rate. As previously mentioned, it is when studied in connection with precipitation and soil

moisture that evaporation can be considered as giving most valuable information concerning the water economy of a plant or a plant community.

Most significant in determining the vegetation of any region are not the average but the extreme conditions which may happen only occasionally. It is at such times that evaporation may become the limiting factor which determines the species able to survive in the alpine zone. Weaver and Himmel (1931) find that it is dry periods when soil water is low and evaporation rate high that are critical for vegetation. Winds by their desiccating action then produce serious injury to plants. A careful study of the climatic factors effective during the summer of 1928 with its frequent summer frosts, its wide daily temperature variations, and its periods of bright, windy, rainless days sheds more light on alpine vegetation in regard to the structure and general habits of growth of its individuals, in regard to the floristic composition of its plant associations, and in regard to the successional relationships existing between its plant communities than does a study of the relatively much more equable climate of the growing season of 1929.

Humidity and soil moisture.—Quantitative work in determination of humidity and soil moisture was not attempted. Only such information was obtained as could be inferred from observation of wind, light, clouds (mists), rate of drying of various objects, and the loss of weight of soils upon drying. The occurrence in a community of one or more species of which the soil water requirements have been pretty well established (Ramaley 1917, 1919) was regarded as giving fairly definite information concerning the water relations in the habitat. Rapid drying of wet vegetation, soil, and other objects following a shower indicates rapid changes in humidity in alpine altitudes.

The humidity factor is important because of its relation to loss of water through transpiration. Weaver and Himmel (1931) in their prairie studies find that soil moisture and humidity are most important factors in determining the species which can succeed. Total precipitation and average humidity are comparatively high in the alpine zone. Ordinarily showers are fairly frequent during the summer, and conditions of humidity and soil water, except for short periods, probably remain within the limits necessary for most of the plants of the region in spite of sudden and frequent fluctuations in humidity and rainfall. It is doubtless during rainless periods, such as occurred in the summer of 1928, accompanied by strong wind, low humidity, and high evaporation rate that soil moisture becomes deficient in exposed situations to a point critical for vegetation.

Soil.—Lack of stability, except on surfaces of moderate relief, prevents the development of alpine soils to anything approaching a state of maturity. Chemical processes are greatly retarded by the slight solubility of the silicate rock. The conversion of large rocks to smaller fragments is accomplished largely by freezing and by differential expansion of the contained minerals.

Activity of both wind and water tends to prevent the accumulation of the finer particles.

In cracks and between boulders soil accumulation may occur much sooner than upon fell fields or slides. In shallow basins, about seepage spots, and along low margins of streams and lakes vegetation and soil develop most rapidly. In such places and on less exposed slopes of moderate relief the vegetation in time almost completely stabilizes the surface. Certain species in each particular habitat act as humus formers so that the organic content of the soil tends to increase in all places which support any form of plant life. With addition of humus soil texture becomes finer. Upon moderate slopes, where soil forming activities have proceeded for long periods with little disturbance, the most mature soils of the region eventually develop.

Since only silicate rocks occur, it will be readily understood why only acid soil reactions obtain. Due to lack of basic materials, such as lime carbonate, the acid condition which develops from decomposition of complex silicates of crystalline rocks and from the growth of plants, is not neutralized. This acidity in combination with low temperature, poor soil aeration, and absence of soil organisms which cause decay promotes accumulation of a peatlike humus poor in plant nutrients. All the soil and even the water may show a distinctly acid reaction. Soils which develop in this manner are characteristic of the alpine zone in all regions lacking calcium carbonate. Humus content varies greatly from rock waste entirely destitute of organic material to moor deposits composed largely of raw humus.

According to Braun-Blanquet and Jenny (1926) alpine humus soils can be recognized by the fact that in their soil profile the A_1 horizon, consisting only of partly decomposed plant parts and windblown mineral matter, exceeds the other horizons. The difference between alpine humus, dry peat, and raw humus is only superficial, the chief criterion for raw humus being its acidity and its finely dispersed condition, which qualities are responsible for the unfavorable properties of unsaturated humus materials. Alpine humus soil is a genuine climatic type and eventually develops at high alpine altitudes irrespective of the geologic substratum, forming in considerable depth on lime as well as on crystalline rock. On lime the evolutionary process is much slower and more complicated. On crystalline rocks the weathered, disintegrated minerals with progressive humus formation and acidification proceed directly to the formation of alpine humus soil, the process being only a matter of time.

Most species of higher plants appear to have a considerable pH range within which they are able to carry on all their vital functions in a fairly normal manner. When other factors of the environment are favorable, the pH range is probably greatest. On tension lines between plant communities where soil water relations, humus content, and other factors are near their limits for certain species of the different communities, it is possible that

pH sometimes becomes the limiting factor in determining the distribution of species. A consideration of soil reaction values in different communities of the region (Table VI) shows that average pH values range from pH 5.0 to 6.4. The lowest soil reactions found were in lichen-moss snowflush community and in polsters on a fell field, where pH values of 4.0 and 4.2, respectively were obtained. Since most communities show soil reactions from pH 5.0 to 6.0, this factor does not appear to have any great significance directly in determining the distribution of the alpine plants in this region. Perhaps its greatest importance lies in its effect upon ionic exchange during the process of absorption of mineral salts and upon the promotion of the general nutrient-poor conditions of alpine soils by preventing the growth of soil organisms which would bring about a more complete decay of plant remains, thereby releasing the supply of nutrient materials bound up in the soil.

TABLE VI. *Soil reactions in alpine plant communities.*

Community	pH
Wind timber; also *Vaccinium* stands	5.2
Sedge moor	5.2
Wet sedge meadow	5.0
Snow flush	5.0
Fell field (Wind communities)	5.0
Climax meadow (Elynetum)	5.6
Salix (S. chlorantha, S. pseudolapponum)	6.0
Salix (S. nivalis, S. saximontana, S. petrophila)	4.8
Dryas octopetala	6.0
Sedum rhodanthum (Shallow streams, wet meadows)	6.0
Boulder field	6.0
Talus slide (no vegetation)	6.4

Table VI summarizes the results obtained from many pH determinations made on soil of different plant communities of the region.

BIOTIC FACTORS

Grazing.—Grazing does not appear to have had a pronounced effect upon the alpine vegetation in this region, but no records are available for comparison of past and present conditions. Certain species of ruderals, *e.g. Polygonum aviculare, P. engelmanni, Chenopodium leptophyllum,* and *Capsella bursa-pastoris,* are found in a relatively limited area on the slopes of a valley used for a considerable number of years as a herder's camp. Sheep, cattle, and horses have frequently been gathered into this valley at nights during the grazing season. Since the plants just mentioned are unusual at this altitude and do not occur generally over the rest of the region, their occurrence is probably connected with the bringing of domestic animals into the area. Whether these species will persist or not remains to be seen. Cattle and horses were probably first brought up to these high altitudes during the early mining activity more than half a century ago. Some grazing has been carried on during summers for twenty or thirty years, but it is only during the last decade that anything like intensive grazing has been practiced.

Grazing by sheep is at present confined mainly to the region above the trees. Cattle graze mostly below tree line. Grazing by horses is at present inextensive.

Due to the severity of conditions normally present, grazing might be accompanied by serious danger of upsetting the natural balance among species in the alpine region sooner than in regions with more favorable conditions for plant growth. In view of the limited extent to which intensive grazing has occurred on James Peak, it seems probable that it has had little influence upon alpine succession here.

Fire.—The effect of fire on vegetation in the alpine zone would be expected to be negligible. In the region about James Peak extensive fires destroyed a great deal of the forest in the subalpine zone in the decade from 1870-80. In places the burned areas extend to the alpine zone. Subalpine zone is potentially forest land while alpine zone is potentially grassland. Severe burning has removed forest and soil, and in exposed situations adjoining the former alpine-subalpine border, has resulted in conditions approximating those characteristic of alpine altitudes. Regeneration of the burned-over area has been slow. In much of the region few trees have appeared in the half century which has elapsed since the fire. On slopes exposed to severe wind action, many alpine pioneers have invaded the burned area, and alpine vegetation is now frequently encountered several hundred feet lower than the former alpine border. *Sieversia turbinata, Silene acaulis,* and *Eritrichium argenteum* are examples of distinctly alpine species now sometimes occurring as low as 10,600 feet, whereas the former timber line is at 11,000 to 11,500 feet. Patches of spruce, fir, and pine forest in a few places escaped the conflagration. These, as well as unburned stumps and prostrate tree trunks, give evidence of the former condition when subalpine forest covered the region and appear in striking contrast to the alpine aspect of the vegetation which sometimes surrounds them.

Clearing (lumbering), Mining.—Cutting of the trees has been almost negligible in its effect on the downward extension of the alpine zone. Had it not been for fire, which left little of the forest to attract the lumberman, this might have been otherwise as the region lying to the east and south of Kingston has been the site of considerable mining activity, which frequently levies a severe toll upon the surrounding forest. Since about 1900, however, mining activities have declined, and the demand upon what little forest escaped the fire has been slight.

VEGETATION

Introduction.—Alpine vegetation consists of the species characteristic of the alpine zone. True alpine plants are characterized by their ability to live in the open region above the trees. Tree species are able to succeed up to a certain height on a mountain slope. Beyond that limit grassland vege-

tation becomes dominant. The border between alpine and subalpine zones is itself commonly a belt of varying width in which these two different types of vegetation contend with one another and with the climate for existence and domination. With changes of climatic conditions this battle zone fluctuates up or down the mountain side. Various factors, such as exposure, slope, and soil, produce considerable differences in the altitude of the border line. There results a very irregular tension zone in which alpine and subalpine individuals and groups intermingle. This tension belt is a transition region between the two zones. It is commonly characterized by dwarfed, deformed tree species which tend to sprawl along the mountainside in the direction of the prevailing wind. This form of vegetation is variously known as wind timber, krummholz, or alpine scrub.

Below the tension zone the region comes eventually to be dominated by subalpine forests. Alpine species in many places have extended their ranges downward, perhaps only temporarily, in areas where fire, deep accumulation of snow, or severe wind have displaced subalpine plants. In places trees and other subalpine plants, aided by favorable conditions, have extended their ranges upward, crowding out, at least temporarily, alpine vegetation. Such fluctuations sometimes make it difficult to classify species as strictly alpine or subalpine. Throughout the present discussion the transition zone is treated as a part of the alpine. In the list of species found in the region plants appearing in the alpine zone only in the transition region are so indicated.

Alpine vegetation as a whole may be conveniently classified into the three distinct types of Schimper (1903): forest, grassland, and desert. The forest is represented only by the wind timber or alpine scrub forest of the transition zone and forms a more or less broken girdle varying greatly in width and in altitude. In this transition area occur alternately patches of scrub and of grassland, the former making up the greater part of the vegetation in the lower portion and the latter occupying the greater part near the upper margin. Where the borderline is approached on steep slopes or where it is marked by cliffs, the wind timber may be lacking and the change between zones may occur abruptly.

The greater part of the vegetation of the alpine zone is of the grassland type and occupies the broad and gentle mountain slopes and valleys above the tree limit. This treeless area is sometimes referred to as alpine tundra (Weaver and Clements 1929). Here occur the alpine meadows. The vegetation varies in floristic composition in accordance with the conditions of the particular habitat. It consists of grasses, sedges, dicotyledonous herbs, and in places it is dominated by shrubs. Seasonal aspects are pronounced at different times during the growing period. This grassland vegetation is best developed in the more favorable places and in its mature state is dominated by a sedge-grass climax.

Much of the alpine zone presents a rather barren aspect at all seasons. Due to the great extent of exposed rock and boulder heaps with little or no soil, much of the surface can, at best, support only a sparse vegetation of pioneer species. Portions of the region which are vegetationless or which possess only a very scant plant population fall within the category of alpine desert. Cliffs, hogbacks, talus slides, and boulder fields frequently extend the desert far below the alpine zone.

Methods.—The methods employed in this study of alpine vegetation and its succession are: (1) acquiring information concerning conditions existing at different stations or habitats throughout the region by instruments and by systematic and detailed observation; (2) determining the floristic composition of the vegetation in the various habitats and the relative abundance of the species in each association by means of a statistical study of the plant population of each habitat; and (3) reconstructing the complete course of vegetational development from its pioneer to its most advanced stages from a study of all these stages in places where they now occur in the region.

Data obtained from the study of the climatic factors were supplemented by observation of the changes taking place in the vegetation throughout the growing season. The results obtained and the conclusions reached from the study of the alpine environment are recounted in the preceding pages. The results of the floristic and successional studies are discussed in the succeeding part of this paper.

The analysis of the vegetation into its fundamental social or synecological units was effected principally by means of a modification of the statistical method as used by Raunkiaer (1918). This method of arriving at a knowledge of plants through a study of their community relationships has been used more extensively by European than by American ecologists. While the feeling is probably pretty general among Americans that some European phytosociologists have overemphasized the importance of the various social relationships in the development of plant communities, it must be admitted that the careful methods of analysis as practiced by central and northern European workers give an intimate knowledge concerning the exact structure and composition of the vegetation and its units and concerning the individual role and relative importance of each species in the community.

In this statistical study quadrats varying in size according to size of plants and density of vegetation were employed. For most of the alpine grassland where plants are small and occur in fairly uniform density, 0.1 square meter quadrats were employed. On fell fields and rock slides where the vegetation was sparse and it was desired to estimate proportion of bare surface as well as the frequency of species, 0.5 square meter was frequently the size used. One square meter was employed in studying dwarf shrub associations dominated by Dryas, *Ribes* spp., and the larger species of Salix. For the tree

species of wind timber a 10 meter quadrat was employed, but for the lower layers in this community the smaller units were used.

In each instance quadrats taken in linear series at uniform distances in places where the association appeared fairly uniform were scored for frequency of species, proportion of bare ground, and proportion of the area covered by each species if this coverage amounted to as much as one-twentieth of the whole. Due to the very prominent habit among alpine species of spreading vegetatively to form mats, cushions, or turf the proportion of the vegetation cover in a given habitat, furnished by a species, is far more significant in the matter of domination of the association than the number of individuals of this species present.

In order to facilitate the work of determining the importance of different species in an association from the standpoint of frequency or constancy of their occurrence, and of the proportion of the total area covered by each, the plan used by Braun-Blanquet and Pavillard (1925) was employed. Five degrees of presence or constancy, also five of covering or dominance are recognized. Each is expressed by the figures 1-5.

In regard to presence the significance is:

1. present in less than 1/5 of quadrats studied
2. present in 1/5 to 2/5 of quadrats studied
3. present in 2/5 to 3/5 of quadrats studied
4. present in 3/5 to 4/5 of quadrats studied
5. present in 4/5 to 5/5 of quadrats studied

In regard to cover the significance is:

1. covering very feeble, less than 1/20 of the area
2. covering 1/20 to 1/4 of the area
3. covering 1/4 to 1/2 of the area
4. covering 1/2 to 3/4 of the area
5. covering more than 3/4 of the area

Attention was given to the matter of periodicity or seasonal prominence of different species, to layering, and to the fidelity or exclusiveness of species with regard to occurrence in one or more associations. Such facts help in arriving at the part played by each species and consequently in determining the importance of the species in the community.

ALPINE SCRUB FOREST; TENSION ZONE COMMUNITIES

The distribution of the alpine scrub in the transition region (Fig. 3) is ultimately determined as the result of the interplay of a complex of environmental factors. Of major importance are the amount of snow and its disposition by the wind. The presence or absence of the tree species appears frequently to be a matter of enough but not too much snow. Sufficient cover is required to protect the branches from the winter winds while the

ground is frozen. Except on rocks, spaces in the tension zone free from wind timber indicate either areas swept free from snow in winter or places where snow accumulates to such depth that the period after the snow melts is too brief to permit the necessary vegetative activities vital to the persistence of tree species. Seed need not be produced every year but must mature occasionally in some parts of the region. The sprawling habit of the woody species results from the weight of the winter snow and from the fact that all branches projecting above the snow are shorn off almost as if by a knife. As a rule, the shearing is an annual occurrence, but occasionally during a winter of deficient snowfall or of unusually severe winds large branches or

FIG. 3. Northeast slope of Kingston Peak. Looking upward across the wind timber zone showing the effect of wind and snow upon the distribution of alpine scrub. Snowflush areas (Schneetälchen) still contain considerable snow. Photographed July 3, 1928.

whole trees may be killed, producing the unsightly appearance frequently noticeable. Late frosts and dry summers add to the number of dead limbs. Fluctuations in amount of snowfall from year to year levy a serious toll upon the woody vegetation. The sand blast effect of wind driven ice crystals as well as the desiccating action of the wind is responsible for the unilateral development of the tree species so noticeable in both alpine and subalpine zones.

Evaporation rates in the shelter of the wind timber and in exposed openings alternating with the scrub, indicate differences in humidity, which are reflected in the varied floristic composition of the vegetation in the two habitats. Plants in the openings are the plants of the alpine meadows above. Plants

in the shelter of the wind timber form a society of less hardy species, many of which are common in subalpine forest below.

The wind timber community is dominated in its mature condition, in more favored locations with respect to snow accumulation, wind exposure, soil, and soil moisture, by a scrub climax of spruce-fir, *Picea engelmanni* and *Abies lasiocarpa*. Dry rocky slopes and windswept ridges, particularly with southwest exposure, are frequently dominated by *Pinus aristata* or *P. flexilis* which appear to form an edaphic climax in places almost destitute of soil and exposed to extreme desiccation by combined action of sun and wind. Where winter snow accumulation is more variable, *P. aristata* may sometimes be the only tree species present. In spruce-fir communities Picea appears to be the more resistant of the dominants. In less mesophytic parts of the community it constitutes a much larger part of the vegetation, sometimes forming almost pure stands. In more mesophytic locations it may give way to almost pure stands of Abies. In pine scrub the same relations hold between *P. aristata* and *P. flexilis*, the former dominating in places with more rigid life requirements. *P. aristata* rarely occurs on north slopes and never in wet locations. *P. flexilis* is much more generally distributed than *P. aristata* in the region and frequently extends downward well into the montane zone.

Thus the four prominent trees of the krummholz may be arranged in a series representing environmental conditions gradually increasing in severity as follows: *Abies lasiocarpa, Picea engelmanni, Pinus flexilis*, and *P. aristata*. As to their upper limits of distribution no consistent difference was observed. In the scrub forest as a whole spruce-fir constitutes a considerably greater proportion of the total area than does pine scrub, the latter constituting more of a fringe about areas occupied by krummholz and dominating locally in less favorable spots. While pine scrub may have acted as a pioneer in some places preceding the appearance of the spruce-fir, there are indications that in many places spruce has been the first of these tree species to invade the slope.

Straggling specimens of *Populus tremuloides, Juniperus communis sibirica*, and *Pinus murrayana* occasionally occur in the wind timber. *Pinus aristata* reaches its northernmost limit of distribution in this area and barely extends into the subalpine zone below the tension line to form a few groves of moderate sized trees.

Of first rank as determiners of conditions of the habitat in wind timber are the tree species. Considering the scrub forest area as a whole, species of the genus Vaccinium are probably next in importance in the maintenance of the community. The Vaccinium layer may be inconspicuous or entirely absent in many places, but this is usually true only in situations more extreme in regard to moisture or light. In much of the wind timber the lower layer is composed of a fairly well-developed carpet, varying in floristic

composition but dominated most frequently perhaps by species of Vaccinium. Quite often small openings between clumps or terraces of scrub also are dominated by *Vaccinium oreophilum* and *V. caespitosum*. Here as in much of the subalpine forest below the same relation appears to hold between the tree species and the accompanying under layer of Vaccinium. But there are many gaps in the Vaccinium society, and locally dominant in these in drier locations are *Polemonium pulcherrimum*, *Chamaenerion angustifolium*, and *Arnica cordifolia*. In the extreme outer edges of the wind timber mats may occur a zonation of *Carex siccata*, several grasses, and many other herbaceous species. Species characteristic of more mesophytic locations are *Pyrola secunda*, *Mertensia ciliata*, *Moneses uniflora*, *Adoxa moschatellina*, *Angelica grayi*, and *Erigeron salsuginosus*. Where shade is rather dense and fallen leaves of conifers form a humid substratum, species of mosses and *Peltigera aphthosa* frequently form a ground layer. The reaction of the soil layer under the krummholz is commonly about pH 5.2. Another shrub layer is frequently more or less distinguishable from the wind timber cover above and the Vaccinium layer below. In drier locations *Salix pseudolapponum* and *Ribes montigenum* develop more noticeably about the outer portions of the wind timber patches; and in wet places between clumps *Salix chlorophylla* and *Ribes coloradoense* frequently occur. With the more vigorous development of these shrubs the lower layers are much reduced.

On wet terraces, which sometimes alternate with the strips of wind timber, sedge moors occasionally develop. On the other hand, exposed openings in the wind timber may exhibit well developed alpine dry meadow vegetation, or if in rocky, windswept situations they may be almost barren, containing only xerophytic species of the fell fields above the tree limit or stands of *Dryas octopetala*, a dwarf shrub of the lower portions of the alpine zone.

Thus it will be seen that the vegetation of this tension zone is a complex in which can be recognized associations of alpine and subalpine zones; and it affords many examples of mixed vegetation representing transitional or tensional communities intermediate in floristic composition between distinctly alpine and subalpine vegetation.

It is of interest to note that here at the extreme upper limit of their range certain species, such as *Carex siccata*, *Chamaenerion angustifolium*, and *Aquilegia coerulea*, which at lower altitudes are characteristic of open areas, occur only in the shelter of wind timber or rocks.

ALPINE DESERT; PIONEER COMMUNITIES

Alpine desert occupies portions of the region which are entirely barren or possess only a sparse vegetation. Under this category are included bare rock surfaces, boulder fields, talus slides, fell fields, and places where late lying snow prevents the growth of plants. Instability of substratum, extreme exposure, low temperature, or unfavorable soil, water, and light re-

lations may be responsible for the continued barrenness. Bare rock surfaces present extreme conditions for plant life. Unstable talus slides are frequently more barren than the surfaces of stable rocks.

"Boulder fields" as here used signifies masses of rocks of various sizes, piled promiscuously but in relatively stable condition. Talus slides are masses of rocks of any size occupying the steeper mountain sides. They are usually in unstable condition, but in mature stages they may become stabilized by vegetation forming meadows where the talus consists chiefly of gravel or finer material. Fell fields are stable rocky areas exposing a considerable proportion of rock surface upon which higher vascular plants are unable to grow. The fell field presents a more even surface so its plants are more uniformly exposed than the vegetation of the uneven boulder field. It will be seen that in all these topographical units which make up the alpine desert the barrenness is outstanding. When vegetation becomes more plentiful, the area enters the category of alpine meadow.

The accuracy of results obtained by the statistical method of determining the floristic composition of the vegetation in a plant community depends largely upon the size of the unit used and on the uniformity of vegetation of the community. In the investigation of these barren areas only the fell field yielded satisfactory statistical data. This was due to lack of uniformity in distribution of the species belonging to any one community which was in turn due to the fact that different habitats frequently occur in such close proximity. Especially is this true of the boulder field. On the rocks themselves the most extreme conditions prevail. In the shelter of the boulders are protected habitats. Water drains from the surfaces of the rocks into cracks where very mesic conditions obtain. Thus the boulder field does not possess a uniform vegetation, but a variety of species from widely different plant associations, the whole constituting a vegetation mosaic. If a small unit is used in analyzing this vegetation, no constants will be found. If a large one is used, the list of constants will include almost all the species on the boulder field. In neither case will the results of the analysis reveal the associations, constants, nor the relative importance of the species which make up the associations. However, the boulder field constitutes a convenient topographical unit for the study of the high mountain region.

Boulder fields.—The xerosere on rocks begins with extremely xerophytic lichens of the genera Lecanora and Rhizocarpon. These are followed by less xerophytic types, such as Parmelia, which tend to overspread and replace preceding species. Irregularities and depressions are etched in the rock surfaces as a result of the dissolving action of substances formed by the plants. Decaying plant remains are added to the substratum, lessening the extreme dryness of the habitat. Low growing, xerophytic mosses in time appear among the lichens and gradually displace them. Accumulations of humus and disintegrating, wind blown rock particles in cracks and crevices,

as well as moss pads, furnish germinating beds for disseminules of vascular species. These pioneer vascular plants find lodgment either on materials deposited on rock surfaces or in cracks and crevices down in the rock itself. The latter positions are less exposed; and species having extremely low humus requirements become established in them. Relative insolubility of silicate rocks limits crevice development, and crevice communities are poorly represented in the region. The following species are commonly found on barren rocks, in cracks, or on ledges where little soil is apparent: *Tonestus pygmaeus, Saxifraga caespitosa, Primula angustifolia, Synthyris alpina, Androsace subumbellata, Luzula spicata, Heuchera parvifolia, H. bracteata,* and *Oxyria digyna.*

Certain species show remarkable ability to establish and maintain themselves among large boulders, forcing their way through narrow cracks among coarse fragments of eroded granite, seemingly in the absence of humus. Some of these are: *Claytonia megarrhiza, Synthyris alpina, Senecio carthamoides, Polemonium confertum,* and *Aquilegia saximontana.* Less exposed boulder slopes near alpine-subalpine border may possess a vegetation in which *Aquilegia coerulea, Mertensia ovata, Sieversia turbinata,* and species of Carex are conspicuous.

Evaporation data taken on a boulder field give little notion concerning water requirements of different plants making up the vegetation. Lichens on bare rocks exposed to desiccation by wind and sun must be extreme xerophytes. Many seed plants too, in exposed positions, with little or no soil accumulation, are pronounced xerophytes. Cushion or mat-forming species characteristic of wind communities on the fell field frequently occur in these exposed locations. But down in the shelter of boulders, especially in positions where water from sloping rock surfaces drains to them during rains, occur mesophytic species such as: *Viola biflora, Aquilegia coerulea, Sedum integrifolium, Carex chalciolepis, C. nova,* and *C. scopulorum.* The last two species are characteristic of wet alpine meadow or of sedge moor associations. In certain places where conditions of light, water, and soil accumulation are favorable, bits of alpine meadow containing species of the alpine climax vegetation may rarely be encountered among embedded boulders. This usually denotes an advanced stage in the development of the boulder field. Erosion and decomposition resulting from the combined action of climate and vegetation tend to wear down the projecting rocks, and where the action of wind and water are not too severe, the accumulation of erosion products and plant remains tends to fill the spaces between the rocks. Vegetation spreads and stabilizes the accumulating products. It appears possible that in the course of time, portions of a boulder field might be transformed to alpine meadow; or where exposure is so severe that the products formed can not accumulate and the barrenness remains, the boulder field might be transformed to fell field with the more uniform and distinctive

type of vegetation of the latter. Boulder fields on the southwest slopes of Kingston Peak suggest the latter type of transformation, while slopes with northern exposure or with shelter from wind occasionally suggest the possibility of the former type. Several species which come to be prominent with increasing density of plant population among the boulders are: *Sieversia turbinata, Claytonia megarrhiza, Festuca brachyphylla, Carex rupestris, Poa rupicola,* and *P. pattersoni.* One or more of these or of a considerable number of other species may assume the leading role at different stages in the succession on the boulder field, but probably no other species does this as frequently and under as widely different conditions as does *Sieversia turbinata.* It appears relatively early among the boulders, has a wide distribution, and succeeds under great variations of exposure and of water, light, and soil relations. During late stages where the boulder field appears to

FIG. 4. Windswept fell field on southwest slope at 12,100 feet showing cushion-mat vegetation. *Trifolium nanum, Arenaria sajanensis, Paronychia pulvinata, Silene acaulis* overspreading the rocks.

be undergoing transformation to meadow Sieversia is frequently the dominant element in the vegetation.

The soil reaction in the various communities occurring among the boulders varies from the slight acidity of the coarse grained granite particles in the absence of humus to the strongly acid reaction of the humus polsters. Determinations made showed a range from pH 6.2 to 4.8.

Fell fields.—Rock rather than vegetation frequently constitutes the greater part of the fell fields. Due to evenness of surface more uniform conditions of exposure prevail than on the boulder field. Stable rock sur-

faces frequently display an abundant flora of xerophytic rock lichens. Well known wind communities (Fig. 4) reach their most striking development on windswept ridges in the mountains. Polster and mat forms, rarely growing more than two or three inches high and presenting a closely shorn appearance, are characteristic of the vegetation in such locations. Several species share extensively and sometimes rather equally the exposed surface in wind communities on James Peak. *Arenaria sajanensis, Paronychia pulvinata, Trifolium nanum,* and *Silene acaulis* may dominate individually or jointly although several other species are characteristic of this community. Warming (1909) gives an excellent description of fell field vegetation. Because of severe exposure, plants with upright habit, unless extremely reduced in stature, rarely succeed in this habitat. Rosette plants, such as *Claytonia megarrhiza, Draba streptocarpa,* and *Saxifraga flagellaris,* are usually present. Grasses and sedges are not prominent but may occur where projecting rocks furnish shelter. The small sedge, *Carex rupestris,* is quite frequently found in these wind communities where it may not exceed an inch in height and rarely appears to fruit. Its ability to spread by rhizomes enables it to maintain itself.

Table VII shows the results of statistical analyses of three typical fell fields. In this, as in succeeding tables, prepared in similar manner to determine the floristic composition of various plant communities, the degrees of presence or constancy, and of dominance or cover are expressed in the columns opposite each species by means of the scheme previously explained. In each column the number preceding the period indicates the constancy and that following expresses the cover or dominance of the species. In case a species is present in any stand but does not occur frequently enough to deserve a rating, it is marked (+). A species occurring in some stands of a given type of community but not in others is marked (—) in the stands in which it is not represented. (Braun-Blanquet. 1932. pp. 68-72).

The evaporation rate on a rather barren fell field at 12,000 feet on Kingston Peak, southwest exposure, was 46.5 cc. per day throughout the period from July 10 to August 26, 1928. This station gave the highest evaporation rate found at any point in the alpine zone and reached an average of 58.4 cc. per day for 10 days from August 17 to August 26. The low cushion or mat form of compact stems greatly reduces the surface exposed to the desiccating action of the wind and also helps to stabilize the substratum and permits accumulation of humus and mineral particles in the interior of the cushion or mat. This sparsely populated plant community constitutes an edaphic climax on the exposed ridges and slopes in many places and may be expected to perpetuate itself as long as climate and soil conditions remain as they are at present. The soil reaction in this community is relatively strongly acid for the region, averaging pH 5.0 and sometimes reaching pH 4.8 to 4.4.

Talus slides.—Talus slides in unstable condition may be without vegetation, even lichens being absent from the shifting rocks. But where, due to moderate slope or to slight addition of material at the source of the slide, the disturbance is decreased, plants with low humus requirement and with special adaptation to the unstable substratum may appear. Certain species with extensively developed root systems and remarkable powers of vegeta-

TABLE VII—*Fell field associations*

	1	2	3
Number of stand	.5 sq. M	.5 sq. M	.5 sq. M
Size of sample	30	30	50
Number of samples scored	13,000	11,500	12,500
Altitude	W	NW	SE
Exposure	4°	12°	10°
Slope	extreme	exposed	exposed
Wind influence	—	4.2	4.6
pH of root layer	30	40	33
Vegetation cover %			
Arenaria sajanensis	5.2	5.2	5.2
Paronychia pulvinata	5.2	5.2	5.2
Trifolium nanum	5.2	5.2	+
Tonestus pygmaeus	3.1	5.1	5.1
Festuca brachyphylla	5.1	4.1	5.1
Sieversia turbinata	3.1	3.1	5.2
Silene acaulis	5.1	2.1	2.1
Artemisia pattersoni	—	5.1	5.1
Selaginella densa	5.1	2.1	+
Claytonia megarrhiza	3.1	5.1	—
Carex rupestris	2.1	+	2.1
Lichens spp.	5.1	+	5.1
Moss spp.	5.1	—	+
Trifolium dasyphyllum	—	2.1	5.1
Eritrichium argenteum	+	+	1.1
Draba streptocarpa	+	1.1	1.1
Phlox caespitosa	—	2.1	+
Saxifraga flagellaris	1.1	2.1	—
Poa rupestris	+	+	+
Luzula spicata	3.1	1.1	—
Lloydia serotina	—	1.1	2.1
Artemisia scopulorum	+	—	1.1
Oreoxis alpina	—	+	1.1
Sedum stenopetalum	+	—	2.1
Elyna bellardi	+	+	—
Saxifraga chrysantha	3.1	—	—
Erigeron pinnatisectus	—	—	2.1
Primula angustifolia	1.1	—	—
Synthyris alpina	1.1	—	—
Androsace subumbellata	+	—	—
Cerastium beeringianum	+	—	—
Lychnis montana	+	—	—
Saxifraga caespitosa	1.1	—	—
Erysimum nivale	+	+	—
Senecio taraxacoides	—	+	—
Calamagrostis purpurascens	—	—	+
Heuchera parvifolia	—	+	—
Actinea lanata	—	—	+
Castilleja occidentalis	—	—	+
Arenaria fendleri	—	+	—
Saxifraga austromontana	—	+	—

tive reproduction are sometimes of local occurrence on these talus slides. The plants sometimes anchor themselves by one or more deep roots extending a considerable distance downward into the more permanent material below and have a rather temporary but extensive root development in the superficial layer of less stable rock waste. The floristic analysis of a slide community usually shows few species even in a fairly well populated community. Great talus slides occur along the sides of Mammoth Gulch, sometimes extending downward for a vertical distance of almost a thousand feet. At certain points on these slopes specialized slide communities are well developed. Two species, *Chamaenerion latifolium and Chaenactis alpina*, were found nowhere in the region except on these slides where they sometimes dominated considerable areas almost exclusively on fine talus in relatively unstable condition. Other species commonly occurring on talus slides in less disturbed spots are: *Senecio holmii, S. taraxacoides, Polemonium confertum, Cerastium beeringianum*, and *Trisetum spicatum*. A limited number of determinations made on the talus slides showed a soil reaction of about pH 6.4. Since plants were very limited in number and there appeared to be no humus present, this reaction would appear to be nearly that due to the decomposition products of the rocks themselves independent of the vegetation.

ALPINE GRASSLAND; ALPINE MEADOW COMMUNITIES

Alpine grassland in the broadest sense includes all the region above timberline which under the present climate will eventually bear a grassland type of vegetation. Thus all the region with a growing season sufficiently long for the maintenance of the flowering plants becomes potential grassland. No place in the Colorado Mountains is too high to support many such species; and in all the areas studied, except unstable slides and stations where snow lies late or where north exposures result in extremely low light intensity, an active vegetation was found. However, there are many places where conditions for plant growth are so severe that an equilibrium between the forces of vegetation and climate appears to have been reached. Gains made by either in one place are offset by losses in another. Where such an impasse is due to certain long enduring conditions of the soil, we have edaphic vegetation types.

According to our modern view soil itself is a product of the climate and undergoes a cycle of evolution similar to that of the vegetation. At each stage in the cycle, soil and vegetation keep pace (Braun-Blanquet, 1932 pp. 255-260). Where soil development is retarded for long periods of time in its progress toward maturity, vegetation likewise is prevented from moving forward to its final or climatic climax condition. In a region as youthful as the Rocky Mountains where forces of erosion are still so active and general instability is so great, it is not surprising that in many places little progress has been made in the development of soil or vegetation.

In accordance with the scheme of classification the meager plant covering of barren rocky areas has been treated as alpine desert. The vegetation here described under alpine grassland consists largely of a series of developmental stages of low herbaceous vegetation frequently referred to as alpine meadow. In these stages plants have come to occupy at least a fairly large proportion of the total surface of the substratum, and the vegetation is characteristically dominated by species of grasses, sedges, and herbaceous plants. Communities dominated by woody species, constituting a scrub vegetation, are not infrequently encountered in different parts of the alpine meadow, and under certain conditions these appear to form an edaphic climax within the grassland area. Other distinctive edaphic communities which occur in the alpine zone are the snow flush meadow and sedge moor.

Several rather definite types of alpine meadow can be distinguished according to the soil moisture condition and to the length of growing season in different places. Where snow lies during all but a few weeks of the summer and the soil is kept saturated with cold water, snow flush communities persist. Where the soil is saturated with water but absence of snow permits a longer growing season of milder temperature, wet meadows or moors with luxuriant vegetation of hydrophytes occur. In places where water relations are favorable during a considerable part of the season but the soil undergoes aeration, the vegetation consists of plants of moderate water requirements and forms a mesophytic meadow. On exposed slopes or in any location where soil moisture is deficient, only plants with low water requirement can grow.

Much of the high mountain region falls into this last category, and the best vegetation possible appears to be a dry meadow composed of xerophytes. As with the wet meadows, two different vegetation types, depending primarily on soil moisture relations, can be distinguished in the dry meadows. The first is the rather sparse meadow, which sometimes appears to be a late stage of development of exposed fell and boulder fields. The second is the somewhat less xerophytic Elynetum or sedge meadow which has been reached on certain of the more stabilized slopes of the mountains. This type appears to be the ultimate or climax vegetation for a large proportion of the region.

Scrub associations.—The woody plants occurring in the alpine zone above timberline include various species of shrubs from several distinct communities growing under widely different environmental conditions. Species of Salix are common in wet stations in all but the higher alpine altitudes. Willows frequently play a part in some stage of development of alpine moor and snow flush floras. Dry stony slopes from timberline to 12,000 feet are often dominated by the low prostrate shrub *Dryas octopetala;* less frequently by clumps of *Dasiophora fruticosa.*

Salix scrub.—Alpine species of Salix can tolerate the severe conditions far above timberline because of ability to endure long submergence in cold

water, to root deeply and extensively, and to complete their life cycle from bud to seed in so short a period. Distribution of the different species is determined chiefly by their different requirements for water and for protection against winter winds. Diminutive species grow where there is insufficient water and winter snow cover for the taller species. All require at least a moist substratum. *Salix petrophila*, *S. saximontana*, and *S. nivalis* rarely exceed 2 to 3 inches in height. They occur on moist gravel slopes and terraces or along stony margins of streams or lakes. They thrive among coarse rock fragments with almost no soil. In such locations they meet little competition with other plants and often form continuous mats. Studded with buds their prostrate stems creep along the surface or burrow beneath the substratum, rooting everywhere. In summer each bud sends up its tiny shoot bearing several leaves and one or two catkins.

Salix monica is slightly taller reaching 6 to 10 inches. This species occurs about the borders of shallow water basins on stony terraces. These depressions hold sufficient snow to cover the stems during winter. *Salix chlorophylla* and *S. pseudolapponum* frequently grow 3 to 4 feet tall in the wind timber where they are most abundant. *S. chlorophylla* grows only about water but *S. pseudolapponum* may occur in any mesic situation since it has by far the lowest water requirement of all these willows.

Salix chlorophylla is usually restricted to the wind timber zone; *S. monica* occurs only above timberline at 11,500 to 12,000 feet. *S. nivalis* is rare. *S. pseudolapponum*, *S. petrophila*, and *S. saximontana* are common from 11,000 to 12,000 feet. In the shelter of the scrub thickets carpets of moss and flowering plants frequently develop. Salix scrub probably represents an edaphic community of long duration on coarse wet gravels in much of the alpine zone. Soil reactions in this community vary from pH 4.8 to 5.6.

In a few locations and always very limited in extent, patches of *Vaccinium orcophilum* are encountered in the alpine meadow above tree line. An extreme case was in a snow pocket at 12,000 feet on a sheltered slope more than 1,000 feet higher than the nearest wind timber a mile away. The occurrence of Vaccinium above the wind timber always appears to be dependent upon a snow cover which melts off by July 1. With such a short growing season it does not thrive; and as it rarely has time to mature seed, it spreads very slowly. Soil reaction in the Vaccinium community averages pH. 5.2.

Dryas scrub.—In the lower alpine zone stony slopes with a limited snow cover in winter but with exposure to wind in summer are often dominated by the small shrub, *Dryas octopetala*. In the wind timber zone insufficient snow accumulation frequently prevents tree species from occupying these slopes. Extreme exposure to wind during summer makes conditions difficult for herbaceous species. The slopes frequently present an irregularly terraced appearance because the shrubby plants tend to stabilize the gravel which is blown or washed down from higher levels. The terracing is probably partly

connected with the creep of the loose surface material down the slope during the melting of snow and during heavy summer showers. Deep rooting by Dryas holds it fast, but the creep inclines the clumps in the direction of movement. The stems of this dwarf shrub appear appressed to the sloping surface while the nearly level stony terrace tops alternate with small sloping Dryas clumps which form discontinuous strips running more or less horizontally along the slopes. Such an arrangement affords shelter from the wind and also makes possible the gaining of some heat by reflection from the rocky substratum. As a result this woody species is enabled to mature its seeds during the short growing period.

The Dryas stand is an open one; and while the shrub is dominant, it commonly has a considerable number of rather constant associates from pioneer rock communities and from the dry meadows. A population study of a typical Dryas slope shows the following species prominent: *Dryas octopetala, Carex rupestris, Actinea lanata, Arenaria sajanensis, A. aequicaulis, A. fendleri, Selaginella densa,* and *Eritrichium argenteum.* The Dryas association forms an edaphic climax on the exposed slopes and appears destined to persist as long as the conditions of wind, snow duration, and rocky soil remain as they are at present. In no case was Dryas found above 12,100 feet on James Peak. Soil reaction in this community was pH 6.0.

Dasiophora fruticosa occasionally occurs on exposed rocky slopes at timberline, and it ascends to 12,100 feet on Kingston Peak. In windswept positions it not infrequently assumes the rounded cushion form so characteristic of wind communities. In a few instances it forms stands capable of dominating the community in which it occurs.

Snow flush associations.—The term "Schneetälchen" was first used by Heer (1836) for localities in regions poor in calcium carbonate where the soil is kept saturated during much of the growing season by water from the late-melting snow cover. The characteristic vegetation in such places is a more or less dense stand of rather low growing turf or sod-forming species. Considerable study has been devoted to snow flush floras by central and northern European ecologists, but little attention has been given to them as definite plant communities of the alpine or arctic vegetation in North America.

Areas on James Peak from which snow usually does not melt before July 1 to 15 exhibit the characteristics peculiar to the snow flush. There appear to be two types of snow flush communities. Where the snow-free period does not exceed four or five weeks, the vegetation is sparse, usually consisting of mosses, lichens, and a few straggling grasses and sedges. Where the snow-free period amounts to six weeks or more, sedges, grasses, and several dicotyledonous herbs are also present. The latter type is much more clearly defined. It is frequently dominated by two or three species. Occasionally a single species forms almost a pure stand. *Carex nigricans* some-

times plays such a role. Other flowering plants prominent in these communities are: *Carex pyrenaica, C. nubicola, C. festivella, C. phaeocephala, C. festiva, Poa pattersoni, Aira caespitosa, Erigeron melanocephalus, E. uniflorus, Poa reflexa, Ranunculus adoneus, Sibbaldia procumbens, Trifolium parryi, Polygonum bistortoides, Sieversia turbinata,* and *Arenaria sajanensis.* The last two plants named above are of common occurrence in fell field and dry meadow. Such species are indifferent to snow cover in contrast to species which, like *Trifolium nanum,* seem to be restricted to the windswept fell fields.

Braun-Blanquet (1926) found that the plants composing the "Schneetälchen" flora of the Alps are species capable of carrying on their vegetative activities at a very low temperature, of completing their seasonal activity

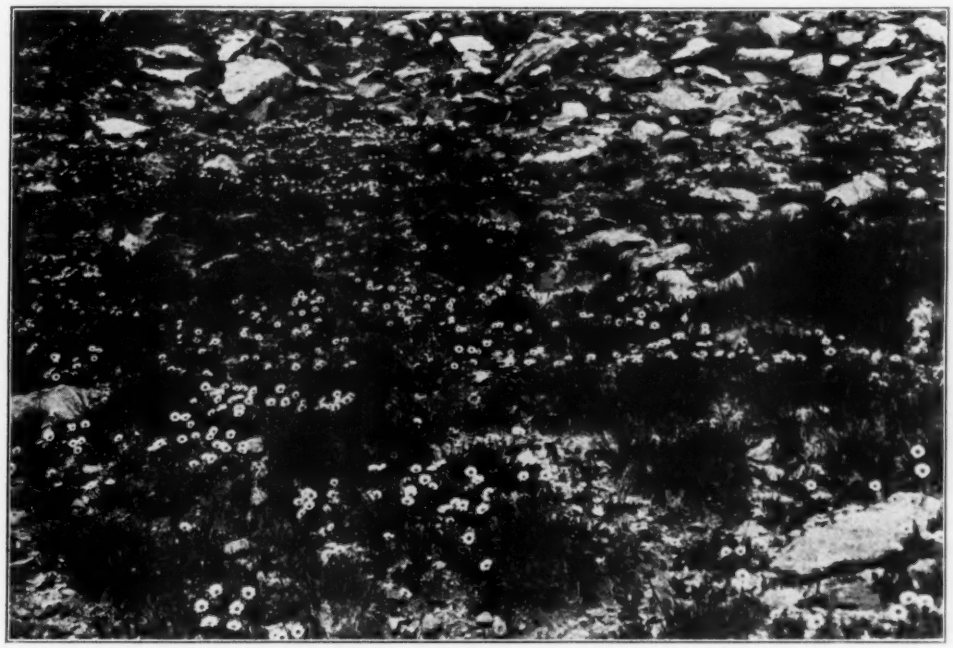

FIG. 5. Snow flush community on east slope of Kingston Peak at 11,500 feet, dominated by *Aira caespitosa, Erigeron melanocephalus,* and *Carex nigricans.*

from bud to seed in a few weeks, and of propagating by vegetative methods since they are not permitted to produce a seed crop in some years. Annuals are never found in this community. Many of the plants pass the winter with green stems and leaves and carry on vegetative activity under the snow when the cover becomes thin in the early summer. On James Peak certain species, like *Ranunculus adoneus* and *Polygonum bistortoides,* not infrequently push their way through the thin snow cover.

Variation in the length of snow-free period in different snow flushes and propagation mainly by vegetative means by the first species to arrive in the habitat explain the frequent occurrence of almost pure stands as well as

the seeming lack of uniformity in floristic composition of different snow flush floras. Similarity of conditions in snow flush and wet meadow during the vernal aspect of the latter account for the presence of several of the same species in both.

The sod-forming species build up a thick layer of fine textured soil consisting of finely eroded minerals and a high percentage of humus. Soil reactions taken in several snow flush communities varied from pH 4.2 to 5.7. The more acid reactions occurred in a moss-lichen community at 12,200 feet.

With a growing season exceeding two months the water level recedes after the snow has all melted. Air enters the soil, the temperature rises, and different conditions develop in the habitat. Species requiring a longer growing season invade the community and replace the typical snow flush vegetation. However, as long as the snow-free period does not exceed two months and the cold water from the melting snow keeps the soil saturated during the most of this time, the snow flush vegetation will continue as edaphic plant communities dominated by the characteristic "Schneetälchen" flora.

Alpine moor associations.— The alpine sedge moor varies in floristic content according to the conditions under which it arises and the stage of its development. The absence from the alpine zone of certain plants, such as sphagnum, which are extremely important in the formation of extensive peat deposits in moors, is probably due to the severity of conditions during the growing season. Exposure to the desiccating action of wind in the absence of tall dense vegetation may be the limiting factor. Sedge moor is represented by sedge meadows which develop in stations watered by melting snow or by rains higher on the mountain. Water relations undergo considerable fluctuations during the season. One or more species of sedge may dominate a wet meadow, the resultant humus accumulation in time tending to bring about conditions resembling the moor. In most cases this development does not proceed very far. In locations more sheltered by surrounding topography or by the growth of the taller species of Salix, wind action is greatly lessened; and with more favorable and uniform water supply, species of mosses and sedges assume a more important role in the community. In time considerable accumulations of humus may result, with conditions more typical of the sedge moor. Species of Salix thus appear frequently to act as pioneers in such a community, helping to stabilize the coarse stony substratum in the beginning of the sere and to make possible later stages in its development.

Sedge moors are best developed along lake margins or along streams where the water supply is maintained more or less constantly. The vegetation tends to advance gradually into the water. A series of developing moors occurs on successive rock terraces near the outlet of James Peak Lake.

Species of Carex and Juncus have constructed restraining barriers at the lower edges of gently sloping terraces where the water spreads out in a thin sheet before falling to the next terrace below. Pools of water are formed on the terraces. The Carex-Juncus dike varies from a few inches to two feet in thickness, and the water seeps slowly through the humus barrier in many places or may overflow it after hard showers. *Carex aquatilis* appears to form most of the reinforcement for this dam; but *Juncus mertensianus* and *J. parryi* act as pioneers of the community. All these species form tenacious sods of underground organs by means of which the enbankment is held in position. Mosses are prominent in the community. On the sloping sides of the narrow valley the vegetation shows a zonation from sedge-rush border at the water's edge to dry alpine meadow on the higher slopes. Overlapping but still distinguishable are the zones quite as described by Ramaley (1920) for high subalpine lake shore vegetation in the region several miles north of James Peak Lake. Mingling with the sedges are individuals of *Salix chlorophylla* and *S. pseudolapponum*. Where the water enters the uppermost basin, washing in more or less gravel, the following stream margin species occur: *Sedum rhodanthum, Cardamine cordifolia, Primula parryi, Epilobium lactiflorum, Juncus mertensianus,* and *J. parryi*. In the sedge community at slightly higher elevation are *Caltha rotundifolia, Trollius albiflorus, Pedicularis groenlandica, Gentiana romanzovii, G. monantha, Swertia congesta, Parnassia fimbriata,* and *Aira atropurpurea*, plants of the wet alpine meadow. In the sedge moor-wet meadow community also occur *Carex illota, C. misandra,* and *C. capillaris*. Representing the heath moor is a zone containing *Kalmia polifolia, Gaultheria humifusa,* and *Vaccinium caespitosum*. Species intermingling with the heath representatives and forming a transition to the upper slopes of dry alpine meadow are: *Aira caespitosa, Veronica alpina, Castilleja lauta, Potentilla diversifolia, Thalictrum alpinum,* and *Zygadenus elegans*.

Many species of the moors which develop in the transition zone on the alpine-subalpine border belong mainly to subalpine zone. It is apparent that conditions for the extensive sedge moor development are more favorable below than above timberline. James Peak Lake lies at 11,090 feet above sea level on the upper border of the transition zone. Alpine species dominate the exposed slopes in the vicinity while in sheltered places alpine and subalpine species intermingle. In the higher alpine altitudes of this region lakes are infrequent. Where they are present, snow and ice last so late that the growing season is too brief to permit the development of more than a sparse vegetation. Consequently, the nearest approach to the sedge moor on the high mountain slopes is usually the wet sedge meadow with its dense accumulation of peat-like material in the substratum. Echo Lake, which is located near James Peak Lake at practically the same altitude, is being in-

vaded in two or three places along its northern margin by a willow-sedge-heath moor formation similar to that just described.

Prominent species of the willow-sedge meadow moor of the higher altitudes are *Salix chlorophylla, S. pseudolapponum, S. monica, Carex nigricans, C. scopulorum, C. variabilis,* and several mosses. Species of less importance, but characteristic of the community are: *Artemisia scopulorum, Sieversia turbinata, Polygonum bistortoides, Sedum rhodanthum, Sedum integrifolium, Gentiana romanzovii, Castilleja occidentalis, Pedicularis scopulorum, Aira caespitosa, Festuca brachyphylla, Poa pattersoni, Juncus subtriflorus, Carex misandra,* and *C. capillaris.* One of the largest and best developed of these higher moors is on the southeast slope of James Peak, at 12,000 feet near the foot of a rather steep terrace which provides considerable shelter from the wind. The willows grow from one to three feet tall in a more or less closed formation, constituting a cover of about 50%. In a lower layer herbs and mosses form a ground cover of about 60% one third of which is mosses. *Carex nigricans, C. scopulorum,* and *C. variabilis* often perform a most important role in the formation of these moors on north exposures or in places where snow lies until July 1. *Carex nigricans* sometimes forms a close compact turf over the water saturated gravel substratum and dominates this association to the exclusion of almost all other species except mosses. With increased growing season the snow flush community sometimes tends to develop into a moor. The soil in moors and sedge meadows has a high humus content and a distinctly acid reaction varying from pH 4.8 to 5.8.

Wet meadow associations.—Border lines between plant communities are perhaps more poorly defined in the alpine zone than in any other region. The short growing season with its rapidly shifting conditions and the close proximity of widely different environments tend to complicate the situation. Embraced in the alpine flora within a relatively small area are most of the families and many of the genera occurring in a lowland region with a wide range of latitude and length of growing season. There is little wonder that this remarkable telescoping of latitudes, seasons, and vegetation into such a small space results in much overlapping of habitats and plant communities and frequently obscures distinctions which are easily observed at lower altitudes. In order to trace the succession it is necessary here as elsewhere to analyze the vegetation into its elementary units and to determine their relation to one another. Difficulty in defining these units frequently makes distinctions set up appear artificial and imaginary. Especially was this found to be true of the different communities and habitats of the hydrosere.

The wet alpine meadow consists of herbaceous species which thrive in soil saturated with water during all or most of their vegetative period. Algae and mosses are of frequent occurrence in streams and stagnant waters. No submerged aquatic flowering plants were observed. Probably few exist

in the cold waters. In lowland regions the vegetation of shallow stream and lake margins is frequently distinctly different floristically from that of the bordering shores even though the latter are water saturated; but at high altitudes in the mountains there is more uniform floristic structure in populations in wet places everywhere. Typical Scirpus-Phragmites-Typha stands do not reach the alpine zone. The nearest approach to such a stage of development is that occurring early in the formation of a sedge moor when a

FIG. 6. Wet meadow community along stream margin dominated extensively by *Mertensia ciliata*, *Primula parryi*, and *Aira caespitosa*.

border of Juncus species sometimes appears. But even this really belongs to the subalpine zone, rarely proceeding across the alpine-subalpine border. Such species as *Cardamine cordifolia*, *Sedum rhodanthum*, *Saxifraga arguta*, *Primula parryi*, *Mertensia ciliata*, *Pedicularis groenlandica*, and *Parnassia fimbriata* sometimes form almost pure stands confined to shallow streams and lake margins (Fig. 6). These may almost be considered to form an aquatic community. The volumes of most streams and lakes of the James Peak region are so changeable that little opportunity is afforded for such

stands to develop extensively; and since these same species occur mingled with the other species of the wet meadow about springs and seepage spots, they scarcely seem to form a distinct community.

In spite of rather obvious differences between wet meadow, snow flush, and alpine moor, the similarity of conditions existing in all three of these communities is indicated by the considerable number of species common to two or to all of them. Following are some examples: *Caltha rotundifolia, Trollius albiflorus, Ranunculus adoneus, Primula parryi, Polygonum bistortoides, Trifolium parryi, Carex scopulorum, C. variabilis, Poa alpina,* and *Aira caespitosa.* Several of these are also prominent in the mesophytic meadow. Environmentally the wet meadow differs from the snow flush in possessing longer growing season, higher temperature during the vegetative period, lower humus content and higher mineral content in the soil, and lower acidity. Wet meadow differs from alpine moor in the last three of these conditions. Floristically wet meadow commonly differs from both these other wet communities in its smaller proportion of grasses and sedges; but there are exceptions. Many species of the wet meadow require a longer growing season than is afforded by the snow flush, and many mature a seed crop during most years. The plants cannot carry on vegetative activities vigorously at such low temperatures as can many snow flush species. Reasons for the lower humus content in the soil of the wet meadow community may be in part less favorable conditions for accumulation of humus in actively flowing water and in part more favorable conditions for the washing in of mineral matter. More rapid destruction of humus may also occur since conditions are more favorable for the activity of bacteria than in the colder snow flush and in the more acid moor. A great difference occurs between the end conditions arrived at by the succession in the wet meadow and in these other wet communities. With building up of the substratum there occurs a lowering of the water table, and wet meadow proceeds directly and continuously through mesophytic meadow and arrives at the climax vegetation of the region. But as long as the climate of the region remains as at present, snow flush and alpine moor, because of peculiar local conditions imposed upon them, appear destined to retain their characteristic types of vegetation.

The volume of alpine streams varies greatly not only at different times of the season but frequently during the course of the day. Many small streams flow continuously during the early part of the season while the snow is melting but in late summer only during periods of frequent showers. A study of the flora about the margin of a stream or lake of variable volume shows a community of species of high water requirements in early summer, while many plants of low water requirements occupy the same location in late summer. Such variable conditions are not limited to stream and lake side. Population studies in several communities repeatedly show well defined

hydrophytes, mesophytes, and even species common in dry habitats growing side by side in the same 0.1 square meter sample plot. Probably the hydrophyte has almost finished its vegetative activity before the xerophyte starts its season's growth.

Such pronounced variations in environmental conditions during the growing period help to bring about the seasonal aspect in the high mountains. Seasonal phases of the vegetation, which are quite distinct in regions with long growing seasons, follow one another in rapid succession in the brief vegetative period which occurs at high altitudes. While they can be distinguished in practically all alpine communities, the seasonal expressions are possibly more marked in the wet meadow than in any other one community. Fairly well defined vernal, summer, and autumnal facies can be distinguished. *Ranunculus adoneus* frequently springs into bloom before the snow has melted away from it; and other species, such as *Polygonum bistortoides* and *Caltha rotundifolia*, force their leafy shoots above the frozen soil, suggesting a prevernal stage. Soon after the snow melts away in June, *Pulsatilla hirsutissima*, *Lloydia serotina*, *Androsace subumbellata*, *Primula angustifolia*, *Eritrichium argenteum*, and *Synthyris alpina* are blooming on the slopes and ridges while *Caltha rotundifolia*, *Trollius albiflorus*, *Ranunculus alpeophilus*, and *Cardamine cordifolia* appear in the shallow water of streams or along their wet margins, giving a well marked vernal aspect to the vegetation of the wet meadow. During July while *Rydbergia grandiflora*, *Trifolium nanum*, *T. dasyphyllum*, *Actinea lanata*, *Sieversia turbinata*, *Arenaria sajanensis*, *Dryas octopetala*, and *Castilleja brachyantha* are blooming in the drier communities, *Sedum rhodanthum*, *Trifolium parryi*, *Saxifraga arguta*, *Sieversia turbinata*, *Polygonum bistortoides*, *Erigeron salsuginosus glacialis*, *Senecio crocatus*, *Pedicularis groenlandica*, *Parnassia fimbriata*, *Mertensia ciliata*, *Viola bellidifolia*, *and Veronica alpina* give expression to the summer phase of the wet meadow.

In August the approach of autumn is announced by a rather monotonous tone over the drier parts of the alpine zone. However, the communities with more favorable water relations are still marked by a considerable display of blossoms. The wet meadow at this time is brightened by *Swertia congesta*, *S. palustris*, *Gentiana monantha*, *G. plebja holmii*, and *G. parryi*, all members of *Gentianaceae*. Species of grasses and sedges are often prominent in this community throughout the growing season because of the favorable water relations. Sometimes they may dominate the vegetation, but this happens less frequently and less completely than in moor and snow flush.

A study of a number of wet meadow populations in different parts of the alpine zone (Table VIII) shows that the domination of this type of community is shared by a considerable number of species, and those which dominate in one wet meadow may be almost or entirely absent from another. Part of this lack of uniformity in floristic composition is due to seasonal

TABLE VIII—*Wet meadow associations*

	1	2	3	4
Number of stand	1	2	3	4
Size of sample	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored	20	20	40	20
Altitude	11,100	11,500	12,500	11,000
Exposure	NW	E	SE	E
Slope	8°	5°	12°	7°
Wind influence	slight	slight	medium	slight
pH of root layer	....	5.4	5.0	5.4
Vegetation cover %	90	90	95	90
Sieversia turbinata	3.2	+	5.3	5.2
Aira caespitosa	2.1	3.1	5.3	5.3
Carex scopulorum	3.1	5.3	2.1	2.1
Polygonum bistortoides	3.1	+	5.2	2.1
Caltha rotundifolia	5.2	5.3	5.2	2.2
Gentiana romanzovii	3.1	+	5.1	5.1
Artemisia scopulorum	4.2	—	5.1	5.1
Trifolium parryi	3.1	+	+	5.1
Pedicularis groenlandica	2.1	+	5.1	2.2
Erigeron salsuginosus	+	2.1	3.1	3.1
Thalictrum alpinum	5.1	—	—	1.1
Moss spp.	+	5.1	5.1	+
Festuca brachyphylla	+	2.1	3.1	3.1
Luzula spicata	2.1	+	+	+
Epilobium lactiflorum	2.1	3.1	+	3.1
Phleum alpinum	—	3.1	+	1.1
Veronica alpina	+	3.1	+	1.1
Trollius albiflorus	2.1	+	—	3.1
Senecio crocatus	2.1	+	1.1	3.1
Chondrophylla americana	1.1	3.1	—	2.1
Swertia congesta	—	2.1	—	2.1
Potentilla diversifolia	3.1	+	—	3.1
Angelica grayi	2.1	1.1	—	+
Gentiana plebeja	3.1	—	—	+
Gentiana monantha	2.1	—	—	+
Saxifraga arguta	2.1	+	—	+
Saxifraga austrina	+	+	—	+
Lloydia serotina	2.1	—	+	—
Poa alpina	+	2.1	+	—
Stellaria longipes	—	2.1	—	2.1
Erigeron uniflorus	2.1	—	1.1	—
Erigeron melanocephalus	2.1	+	+	—
Viola bellidifolia	2.1	—	—	+
Cardamine cordifolia	2.1	+	—	+
Primula parryi	2.1	+	—	+
Carex nigricans	—	2.1	—	+
Sedum rhodanthum	2.1	+	—	+
Senecio triangularis	2.1	+	—	—
Mertensia ciliata	+	—	—	+
Ranunculus alpeophilus	+	—	—	+
Valeriana acutiloba	2.1	—	—	+
Sagina saginoides	+	+	—	—
Stellaria umbellata	+	—	+	—
Juncus parryi	—	+	—	+
Juncus subtriflorus	—	+	—	+
Juncus castaneus	+	—	—	+
Pedicularis grayi	+	—	—	+
Parnassia fimbriata	—	—	—	+

shifting of borderlines between communities and to the fact that the population studies in the different locations were made at different times during the season. All species do not appear at the beginning of the growing period. Some complete their vegetative activity in a short time then die down and so may easily be missed in a study made later in the season. The following may be regarded as species which rank high in their importance and in the frequency of their occurrence in this community: *Caltha rotundifolia, Sieversia turbinata, Polygonum bistortoides, Gentiana romanzovii, Artemisia scopulorum, Aira caespitosa, Erigeron salsuginosus glacialis, Pedicularis groenlandica, Trifolium parryi, Epilobium lactiflorum, Festuca brachyphylla, Senecio crocatus,* and certain species of mosses.

Where conditions are favorable for deposition by water and wind, the soil layer is rather rapidly built up by accumulation of inorganic and organic deposits. With the sinking of the water level beneath the soil surface, species of plants with lower requirements invade the wet meadow community. Its population undergoes a change floristically, and characteristic hydrophytes gradually drop out. Species characteristic of the mesophytic meadow, and finally those of the climax vegetation, become prominent and in turn dominate the changing community.

Soil acidity determinations in a number of stream and lake margin communities with wet meadow floras gave results varying from pH 6.0 to 5.2

Mesophytic meadow associations.—Differing from the wet meadow in the water relations existing in the soil, this community frequently occurs as a transition stage between wet and dry meadow. Mesophytic meadows may occur on slopes in the midst of boulder fields, or they may be surrounded by climax or dry meadows in complete absence of wet meadow vegetation. Water from higher on the mountain probably comes close to the surface of the ground in these places. Slopes sheltered from the direct rays of the sun or from the wind are likely to be suited to the plants of this community, most of which do not endure long continued submergence of their root layer during the growing season. Exposed slopes are subjected to too excessive drying during much of the vegetative period.

Examples of mesophytic meadows on moderately exposed slopes occur on the northwest slopes of James and Parry Peaks at 13,000 feet (Fig. 7). Wind prevents extensive snow accumulation and northerly inclination tends to prevent extreme desiccation. The moist soil supports a rather luxuriant vegetation of the meadow type which is frequently dominated by *Poa pattersoni. Sieversia turbinata, Claytonia megarrhiza, Gentiana romanzovii, Carex atrata, Juncus triglumis, Luzula spicata,* and *Synthyris alpina* are prominent while a number of pioneer species of adjoining boulder and fell fields are present apparently as "holdovers" from preceding stages of the succession. Slopes at similar altitude on southern or southwestern exposures are usually occupied by rather barren boulder or fell fields except along

streamsides. Eastern exposures are more likely to have considerable snow accumulations, and the type of community present depends upon rockiness of the slope and length of time it is free from snow.

In moist places at lower elevation in the alpine zone two types of mesophytic meadow are common. One of these frequently borders stream or lake margins and appears to be more or less in the nature of a transition stage in the succession intermediate between wet meadow or snow flush and the climax meadow community. The other occurs in places on dry slopes where water from higher on the mountain comes close to the surface and seepage areas may be present in early season. Prominent in both are cer-

FIG. 7. Mesophytic meadow community on northwest slope of Parry Peak at 13,000 feet, dominated by *Claytonia megarrhiza*, *Gentiana romanzovii*, and *Poa pattersoni*.

tain species of sedges and such dicotyledons as *Sieversia turbinata*, *Polygonum bistortoides*, *Trifolium parryi*, *Artemisia scopulorum*, *Gentiana romanzovii*, *Potentilla diversifolia*, *Veronica alpina*, *Polygonum viviparum*, *Erigeron uniflorus*, and *Castilleja occidentalis*. On mesophytic rocky slopes which may represent late stages of a boulder field, *Aquilegia coerulea* is sometimes quite conspicuous along with sedges, *Sieversia turbinata*, and other species which give the community a meadow-like aspect. Sedges occurring in the mesophytic meadow are: *Carex nova*, *C. chalciolepis*, *C. atrata*, *C. misandra*, *C. capillaris*, *C. nigricans*, and *Elyna bellardi*. Mesophytic meadows, in locations more or less favorable for snow accumulation, tend to lose the characteristics distinguishing them from snow flush communities. Some of the species in this community may be regarded as "hold-

overs" from wet meadow in places where the latter has preceded the present stage of succession. On the other hand, where snow does not accumulate and soil water becomes deficient early, *Elyna bellardi* and other species of the climax meadow may constitute a considerable proportion of the vegetation.

In lower portions of the alpine zone and in openings among the wind timber one occasionally encounters mesophytic meadow of a still different type due to the presence of a considerable proportion of species of grasses which are either quite locally distributed or which seldom form stands sufficiently extensive to impress their stamp upon the community. *Aira caespitosa* and *Poa alpina* are likely to be present from preceding communities of the hydrosere. But on moderately mesophytic slopes grassy meadows are occasionally encountered in which one or a number of the following species are prominent: *Festuca brachyphylla, Trisetum spicatum, Phleum alpinum, Poa rupicola, P. grayana, P. reflexa, Agrostis hiemalis, Calamagrostis canadensis, Aira atropurpurea, Trisetum wolfii, Agropyron tenerum,* and *Festuca rubra.* These species may intermingle with the sedges and dicotyledons as a minor element, or at times they may dominate the community. *Festuca brachyphylla* and *Poa rupicola* are among the most widespread species of the alpine zone and appear in several communities, but they rarely form stands of any considerable extent. Mesophytic grassy meadows appear for the most part to be poorly developed in the alpine zone in the James Peak region and form a rather inconspicuous element in the vegetation. The Cyperaceae are of much greater significance than the grasses in the alpine succession in both hydro- and xero-seres.

Population studies made in five different mesophytic meadow communities are summarized in Table IX. These show that along with such species as *Polygonum bistortoides, P. viviparum, Trifolium parryi, Festuca brachyphylla, Poa alpina, Phleum alpinum, Trisetum spicatum, Potentilla diversifolia, Artemisia scopulorum,* and *Veronica alpina,* which perhaps reach their best development in this community, are a number of species characteristic of wet meadow and snow flush and several which are more characteristic of the climax meadow.

Gradual building up of the soil level and decrease in soil water are accompanied by the dropping out of the more mesophytic species and make possible the invasion of the community by plants of lower moisture requirement. In time *Elyna bellardi* usually appears, and as a result of the progressive dominance by invading species, the meadow assumes a less mesophytic and a more monotonous aspect. Less exposed slopes with short growing season or more favorable water relations may retain indefinitely the mesophytic element in their vegetation and may not yield to the invasion by *Elyna bellardi* and other climax meadow species. Soil reactions determined

TABLE IX—*Mesophytic meadow associations*

Number of stand	1	2	3	4	5
Size of sample	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored	30	20	20	30	20
Altitude	11,100	11,400	11,700	12,500	13,200
Exposure	NW	E	N	SE	N
Slope	10°	10°	30°	8°	20°
Wind influence	slight	moderate	slight	slight	moderate
pH of root layer	—	5.4	—	5.2	5.2
Vegetation cover %	90	90	100	95	80
Sieversia turbinata	5.3	3.1	5.3	5.1	5.3
Trifolium parryi	2.1	5.2	5.2	5.2	—
Aira caespitosa	2.1	5.3	2.1	5.2	—
Polygonum bistortoides	2.1	5.2	3.2	5.2	—
Artemisia scopulorum	4.1	3.1	5.1	5.2	5.1
Gentiana romanzovii	3.1	2.1	4.2	2.1	5.2
Lloydia serotina	3.1	2.2	5.1	3.1	—
Polygonum viviparum	5.2	3.1	5.2	—	—
Poa alpina	4.2	5.2	—	3.1	—
Festuca brachyphylla	3.1	2.1	4.1	3.1	2.1
Thalictrum alpinum	5.2	+	3.1	—	—
Moss spp.	5.1	—	5.1	—	5.2
Elyna bellardi	2.1	2.1	3.1	1.1	+
Trisetum spicatum	+	2.1	2.1	1.1	—
Erigeron uniflorus	1.1	2.1	+	3.1	—
Carex scopulorum	4.2	—	2.1	3.1	—
Potentilla diversifolia	2.1	3.1	+	+	—
Poa pattersoni	—	+	—	—	5.3
Saxifraga chrysantha	—	—	—	—	5.1
Castilleja occidentalis	1.1	—	2.1	2.1	—
Primula angustifolia	1.1	—	2.1	—	2.1
Salix petrophila	2.1	+	—	—	—
Salix saximontana	3.1	+	+	—	—
Luzula spicata	2.1	1.1	2.1	+	3.1
Carex rupestris	+	—	2.1	—	2.1
Swertia congesta	3.1	+	1.1	—	—
Stellaria longipes	1.1	+	2.1	—	—
Erigeron melanocephalus	—	3.1	—	3.1	—
Veronica alpina	1.1	2.1	2.1	—	—
Draba crassifolia	+	+	—	2.1	—
Silene acaulis	1.1	—	+	—	2.1
Trifolium nanum	+	—	+	—	2.1
Gentiana plebeja	3.1	+	+	—	—
Phleum alpinum	+	2.1	—	+	—
Lewisia pygmaea	—	—	—	2.1	1.1
Arenaria sajanensis	—	+	—	+	+
Castilleja lauta	+	—	—	—	—
Castilleja rhexifolia	+	+	—	—	—
Chondrophylla americana	3.1	+	—	—	—
Solidago decumbens	+	2.1	—	—	—
Erigeron salsuginosus	—	2.1	+	—	—
Carex misandra	1.1	+	—	—	—
Mertensia ovata	2.1	2.1	—	—	—
Gentiana monantha	3.1	—	+	—	—
Sibbaldia procumbens	—	—	+	1.1	—
Sedum integrifolium	1.1	3.1	—	—	—
Stellaria umbellata	+	—	—	2.1	—
Poa grayana	+	+	—	—	—

in a number of mesophytic meadows varied from pH 5.0 to 6.0 and averaged about pH 5.4.

Dry meadow associations.—Even at its best a large proportion of the alpine zone appears capable of supporting only a rather poor vegetation. After long ages of struggle between the forces of climate and vegetation, exposed areas of any considerable relief commonly bear but a scanty, poorly developed soil and a meager and rather monotonous vegetation, which might be described as an impoverished dry meadow. The evaporation rate at a station maintained in this dry meadow at 11,500 feet, southwest exposure, was 36.7 cc. per day for the period from July 12 to August 25, 1928. During some weeks the daily rate was considerably higher. In view of the moisture conditions which must obtain in a coarse grained soil, poor in humus and spread in a thin layer on the rocky slopes, the effect of this high evaporation rate, during a week of rainless weather in late July, goes far toward explaining the scanty vegetation. In spite of a relatively high rainfall and humidity much of the region presents conditions for plant life approaching those of deserts in severity. Under the best conditions that can ultimately obtain the vegetation must therefore consist of plants adapted to xeric conditions.

The small sedge, *Carex rupestris*, possesses to a remarkable degree the qualities necessary for success under these rigid conditions. Small size and xerophytic structure give it a low water requirement. The habit of rooting deeply and branching underground enables it to secure moisture and to stabilize its habitat. Low humus requirement permits it to come as a pioneer into the habitat, and vigorous vegetative activity enables it to spread quickly. It requires no snow protection, so on sunny slopes it has the full season for vegetative propagation. Low stature, upright habit, and the tiny space it requires, enable it to succeed in the closely appressed vegetation of wind communities or among the thin stands of somewhat taller vegetation of less exposed stations. *Carex rupestris* occurs on boulder field, on stable slides, on fell fields, in Dryas communities, and is a constant species in dry meadow and in poorer parts of the climax alpine meadow. Except for the very beginning of the xerarch succession on bare rock, this species persists throughout the xerarch sere, and while never found in wet communities, it sometimes occurs in mesophytic meadows kept free from snow cover.

Probably next in importance in the dry meadow community is *Sieversia turbinata*. It too appears adapted for withstanding a wide range of environmental conditions. It appears on the boulder field, and while its larger size and upright habit render it less suited to exposed stations, it commonly occurs in all but the most exposed fell fields. The limiting factor in its distribution in several communities appears to be the snow cover. Sieversia apparently is favored by snow protection during the winter months and tolerates a covering to mid-July or possibly later. It is a good stabilizer and appears relatively indifferent to humus. Besides persisting throughout all but

the initial stage of the xerosere, it is also present in all stages of the hydrosere except in aquatic communities. Sieversia is a constituent of wet gravel communities dominated by Salix and remains important through all the later stages of the hydrosere. It frequently occupies a conspicuous place in the climax meadow in less extremely exposed situations.

While these two species have many associates, the latter vary greatly according to conditions existing in the habitat. Cushion-mat forming species are common, but *Carex rupestris* and *Sieversia turbinata* are of a high degree of constancy and of greatest constructive importance in this association (Fig. 8), which endures on dry slopes for long periods of time. Ultimately improved soil conditions lead to a somewhat less xerophytic meadow, which constitutes the climax vegetation for much of the region. The dry meadow then appears on exposed slopes as a transition

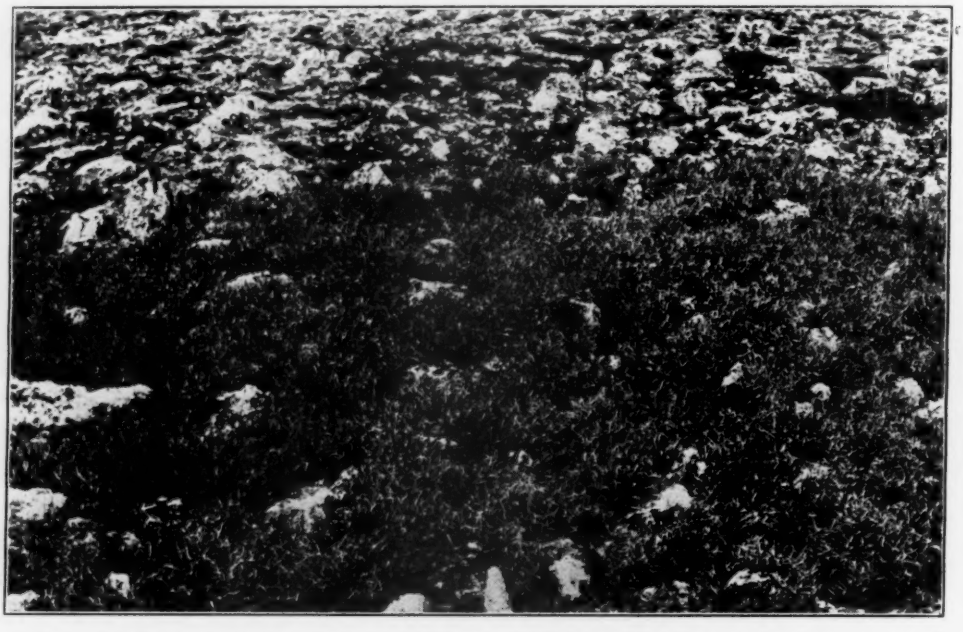

FIG. 8. Dry meadow. *Carex rupestris* and *Sieversia turbinata* invading a fell field and transforming it to the rather impoverished dry sedge meadow.

stage in the xerosere between the pioneer communities of the alpine desert and the climax sedge meadow. The particular type of community preceding it is frequently revealed by statistical analysis of the vegetation, as well as by indications from topography and surrounding associations. The plants making up the association consist largely of species from these pioneer communities although some newcomers appear on account of the changed conditions in this habitat.

Important species in the alpine dry meadow are: *Carex rupestris, Sieversia turbinata,* lichens, *Arenaria sajanensis, Elyna bellardi, Festuca brachyphylla, Eritrichium argenteum, Selaginella densa, Phlox caespitosa, Silene*

TABLE X—*Dry meadow associations*

	1	2	3
Number of stand			
Size of sample	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored	30	20	20
Altitude	12,500	11,700	11,500
Exposure	E	SW	SE
Slope	7°	10°	15°
Wind influence	strong	strong	strong
pH of root layer	4.6	5.2	5.6
Vegetation cover %	60	70	50
Carex rupestris	5.2	5.2	5.2
Sieversia turbinata	5.2	5.2	1.1
Arenaria sajanensis	5.2	5.2	5.2
Silene acaulis	3.2	5.2	1.1
Paronychia pulvinata	5.2	1.1	2.1
Lloydia serotina	3.1	5.1	5.1
Artemisia pattersoni	3.1	3.1	5.1
Eritrichium argenteum	2.1	5.1	3.1
Selaginella densa	2.1	5.1	2.1
Phlox caespitosa	1.1	5.1	2.1
Trifolium dasyphyllum	5.2	—	1.1
Lichen spp.	5.1	5.1	5.1
Festuca brachyphylla	4.1	1.1	1.1
Erigeron pinnatisectus	4.1	3.1	+
Polygonum viviparum	—	5.1	1.1
Oreoxis alpina	3.1	3.1	2.1
Tonestus pygmaeus	4.1	—	2.1
Actinea lanata	1.1	3.1	4.1
Luzula spicata	3.1	2.1	+
Artemisia scopulorum	1.1	2.1	+
Draba streptocarpa	+	3.1	1.1
Elyna bellardi	+	2.1	3.1
Calamagrostis purpurascens	+	1.1	3.1
Arenaria fendleri	+	3.1	3.1
Saxifraga rhomboidea	—	4.1	+
Poa rupicola	2.1	1.1	2.1
Campanula uniflora	—	+	2.1
Campanula rotundifolia	1.1	—	2.1
Potentilla saximontana	—	+	2.1
Allium pikeanum	—	—	5.1
Erysimum nivale	—	+	+
Arenaria aequicaulis	—	—	2.1
Castilleja brachyantha	—	—	2.1
Trifolium nanum	—	1.1	—
Primula angustifolia	—	1.1	—
Sedum stenopetalum	1.1	—	—
Avena mortoniana	1.1	—	—
Castilleja occidentalis	1.1	—	—
Rydbergia grandiflora	+	+	—
Thlaspi coloradoense	1.1	+	—
Agropyron tenerum	+	—	—
Sedum integrifolium	+	—	—
Dryas octopetala	—	—	1.1
Dasiophora fruticosa	—	—	1.1

acaulis, *Saxifraga rhomboidea*, *Polygonum viviparum*, *Lloydia serotina*, *Artemisia pattersoni*, *Oreoxis alpina*, *Draba streptocarpa*, *Erigeron pinnatisectus*, *Actinea lanata*, *Artemisia scopulorum*, and *Poa rupicola*. In meadows with north exposure conditions are less severe due partly to winter snow

cover and partly to somewhat better moisture relations during the growing season. Here Sieversia and certain other plants are more prominent than on south or west exposures. Some species which play a much more important role in these protected stations are: certain mosses, *Sieversia turbinata, Festuca brachyphylla, Thalictrum alpinum, Luzula spicata, Polygonum viviparum. Carex rupestris* and *Elyna bellardi* may be present. Soil reactions in many dry meadow communities show an average acidity of pH 5.6. Table X summarizes population studies made in three typical dry meadow associations.

FIG. 9. *Elyna bellardi* and associates invading *Carex rupestris-Sieversia turbinata* dry meadow and converting it to alpine meadow climax, Elynetum.

Climax alpine meadow association; Elynetum.—Accumulation of humus and increased stabilization of the soil layer make conditions less severe for plant development in the dry meadow. A floristic study of this meadow in many places indicates that a larger and larger proportion of the increasing plant cover is furnished by *Elyna bellardi* as mature stages of the meadow develop (Fig. 9). A similar study of mesophytic meadows indicates that with gradual decrease of soil moisture in the habitat, Elyna and other species from the dry meadow make up an increasing proportion of the vegetation.

Mesophytic alpine meadow, therefore, comes eventually to be invaded by species with lower moisture requirements. The conflict between the mesophytic vegetation consisting of such species as *Aira caespitosa, Poa alpina, Festuca brachyphylla,* and *Polygonum bistortoides* on the one hand and *Elyna bellardi* and its associates from the dry meadow on the other is a long

one. Extreme conditions of climate, most decisive probably in periods of little precipitation and high evaporation during the growing season, favor the species of lower water requirement. The mesophytes drop out gradually in more exposed situations, their places being occupied more and more by the xero-mesophytic Elynetum.

The sedge-like *Elyna bellardi* forms an extremely tenacious sod by means of which it appears to be able, once it gains a foothold in this community, to defend itself against dislodgment by its competitors and to spread and dominate the association. Other sod forming species are rare in a well developed climax meadow. And yet, Elyna at its best forms a thin ground cover with small openings between the tufted plants. It rarely covers more than 60 to 80% of the surface and frequently occupies less. Viewed from above and close up, the surface of the meadow presents a rough uneven appearance since the tufts of sod project slightly above the surface of the ground. As a result of deposition in the tufts and erosion between them, the depressions between these tufts may reach a depth of 1 to 2 inches. The unevenness is sometimes increased by the dying of old tufts. When viewed from a distance, however, the meadow presents a smooth, even appearance. The stems of Elyna may vary in height from 3 to 6 inches, depending on the degree of exposure to wind and sun. Mingled with taller vegetation they may exceed this height. In its general appearance, Elynetum, in contrast with the wet streamside and mesophytic meadows, presents a rather monotonous aspect. While a number of its species have attractive flowers during early summer, the plants are so scattered and in most cases so reduced in stature that they are usually inconspicuous in the meadow. Seasonal change is reduced to a minimum in this Elyna dominated association. In late summer and in early spring the dead or faded stems add to the dullness of the landscape.

In the thin stands of the Elynetum, which are more noticeable on exposed slopes, occur a considerable number of members of the dry sedge-Sieversia meadow. In many cases these are considerably reduced in size, are of cushion or rosette form, and spring from a prominent taproot. The plants nestle in the small depressions between the tufts which are so characteristic of the climax meadow. Species appearing quite consistently in such situations are: *Carex rupestris, Sieversia turbinata, Arenaria sajanensis, Selaginella densa, Eritrichium argenteum, Draba streptocarpa, Actinea lanata, Lloydia serotina, Artemisia scopulorum, Luzula spicata, Trifolium dasyphyllum, Primula angustifolia,* and *Tonestus pygmaeus.* In larger spaces from which they have either never been displaced or in which some destructive agent has made an opening, large polsters and plants of various habits, as well as the preceding species, occasionally appear. Some of these are: *Silene acaulis, Paronychia pulvinata, Calamagrostis purpurascens, Avena mortoniana, Festuca brachyphylla, Poa rupicola, Artemisia pattersoni, Ore-*

oxis alpina, Erigeron pinnatisectus, Sedum stenopetalum, Campanula uniflora, and *Rydbergia grandiflora.*

On north slopes and in more mesophytic spots generally throughout this community *Elyna bellardi* does not compete so successfully with other species. Indeed, in such places the leading role may not infrequently be taken by *Sieversia turbinata.* Other species sharing in a conspicuous way in the community under such conditions are: *Polygonum bistortoides, P. viviparum, Aira caespitosa, Festuca brachyphylla, Poa pattersoni, Oreoxis alpina, Trifolium parryi,* and *Sedum integrifolium.* Inability of Elyna to dominate these stations may follow because a higher soil moisture content enables mesophytic species to grow more vigorously, while Elyna finds optimum conditions at somewhat lower soil moisture where it encounters less competition with mesophytes.

Of primary importance in determining the distribution of Elyna and Sieversia, in fact of most of the plants of the alpine zone, is the matter of snow cover and length of growing season. Best developed Elynetum occurs on areas where little or no snow accumulates and the growing season is at least ten to twelve weeks long (Figs. 10, 11). Elyna appears to be snow avoiding while Sieversia develops best where it has winter snow cover and may occur where late lying snow reduces the growing season to six or seven weeks. Even in rather mesophytic locations on north slopes Elyna is often prominent and sometimes assumes the leading role in the community where snow melts early. Species occurring in both somewhat mesophytic and in drier, more exposed parts of the climax meadow are: *Carex rupestris, Polygonum viviparum, Oreoxis alpina, Trifolium dasyphyllum, Tonestus pygmaeus,* and *Silene acaulis.*

Elynetum may develop at any altitude above timberline but occurs most extensively between 11,000 and 12,000 feet on relatively mature and stable soils of intermediate water relations and moderate exposure. It is not more widespread because so small a proportion of the region has reached the stage of development suited to the climax meadow. Soil reactions in many well developed areas of this community showed a variation from pH 5.4 to 6.0 with best development of the association at about pH 5.6. Table XI summarizes studies made of five stands of climax meadow of different altitudes, exposures, and degrees of slope. These examples emphasize the consistent floristic composition of the association, the relatively large degree of dominance exercised by Elyna in spite of its incomplete cover, and the apparent inability of the companion species to offer serious competition to Elyna.

The development of a climax association of a xerophytic character in the alpine region with its relatively high precipitation and humidity may be questioned. If due consideration be given to the magnitude of the forces involved and to the severity of the conditions which must always exist at this high altitude, even after the theoretical equilibrium between climate, soil, and

FIG. 10. *Elyna bellardi* dominating large expanse of stable alpine area on James Peak at 12,000 feet. Small depressions show where erosive action of the wind has torn out holes in the soil.

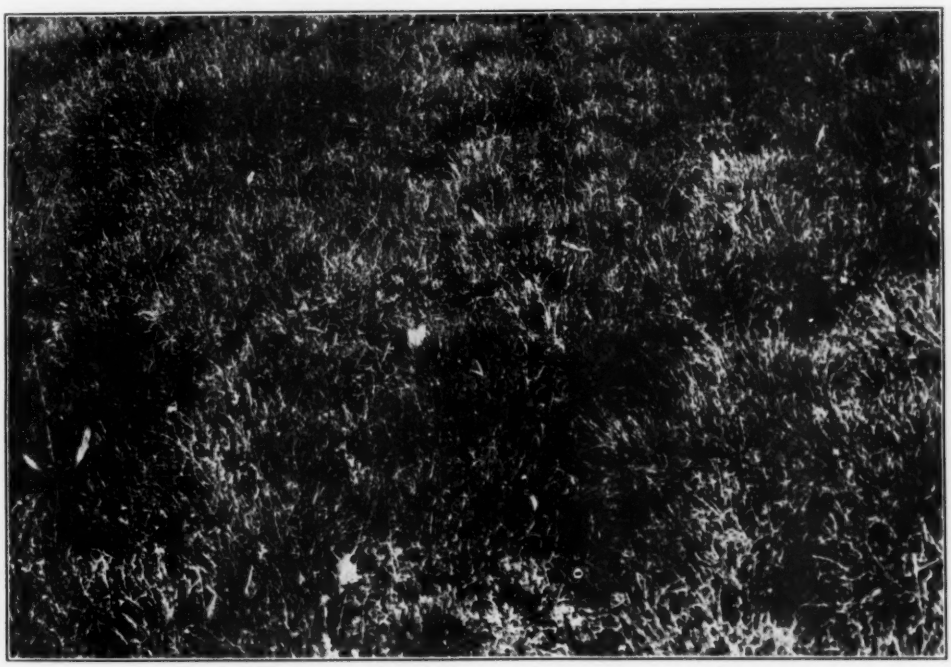

FIG. 11. Elynetum. Detail showing unusually luxuriant development of *Elyna bellardi* in a somewhat mesophytic portion of the alpine meadow climax.

TABLE XI—*Alpine Meadow Climax: Elynetum*

Number of stand	1	2	3	4	5
Size of Sample	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored	20	40	20	20	20
Altitude	11,900	11,300	11,700	13,000	11,800
Exposure	S	E	N	SE	SW
Slope	5°	8°	20°	8°	10°
Wind influence	exposed	exposed	moderate	exposed	exposed
pH of root layer	5.6	6.0	5.4	5.4	5.6
Vegetation cover %	85	85	90	85	85
Elyna bellardi	5.4	5.3	5.3	5.4	5.3
Carex rupestris	5.1	5.1	5.1	5.1	5.2
Sieversia turbinata	5.1	3.1	5.2	5.1	3.1
Polygonum viviparum	5.1	5.1	5.1	1.1	2.1
Lloydia serotina	5.1	5.1	5.1	4.1	3.1
Selaginella densa	5.1	4.1	1.1	3.1	4.1
Arenaria sajanensis	2.1	5.2	1.1	4.1	3.1
Campanula uniflora	1.1	5.1	3.1	—	4.1
Actinea lanata	1.1	5.1	+	—	+
Eritrichium argenteum	1.1	1.1	+	3.1	1.1
Silene acaulis	1.1	1.1	1.1	4.1	+
Luzula spicata	1.1	1.1	+	1.1	1.1
Oreoxis alpina	+	+	+	+	5.1
Poa rupicola	+	2.1	1.1	+	+
Trifolium dasyphyllum	+	—	2.1	+	2.1
Trifolium nanum	+	+	—	4.1	+
Festuca brachyphylla	+	1.1	+	+	+
Artemisia pattersoni	+	2.1	1.1	—	—
Thalaspi coloradoense	+	+	—	+	+
Saxifraga rhomboidea	+	+	—	+	3.1
Rydbergia grandiflora	+	—	+	+	1.1
Castilleja occidentalis	+	—	+	—	+
Arenaria aequicaulis	—	1.1	+	+	+
Arenaria fendleri	—	1.1	—	+	+
Sedum stenopetalum	—	2.1	—	+	+
Primula angustifolia	+	—	2.1	5.1	—
Potentilla saximontana	+	—	—	+	+
Cerastium beeringianum	+	—	+	+	—
Draba streptocarpa	—	+	—	+	+
Tonestus pygmaeus	+	—	—	2.1	—
Polygonum bistortoides	—	—	+	—	+
Aira caespitosa	1.1	—	+	—	—
Dryas octopetala	—	+	1.1	—	—
Erigeron pinnatisectus	—	1.1	—	+	—
Erysimum nivale	—	—	—	+	+
Phlox caespitosa	—	—	—	+	1.1
Saxifraga flagellaris	+	—	—	—	+
Trisetum spicatum	—	—	+	+	—
Gentiana romanzovii	—	—	2.1	+	—
Trifolium parryi	—	—	3.1	—	—
Castilleja brachyantha	—	+	—	—	—
Thalictrum alpinum	—	—	1.1	—	—
Paronychia pulvinata	—	—	—	2.1	—
Allium pikeanum	—	3.1	—	—	—

vegetation shall have been reached, it seems reasonable that rather xeric conditions must always prevail over most of the region and that the only vegetation fitted to succeed would be composed largely of xero-mesophytes. In regard to the soil reaction which will ultimately exist, it appears reasonable to

conclude that since the soil arises from silicate rocks which are deficient in basic materials and since the action of both climate and vegetation tend to increase this acidity, the final product can not be other than acid. In the Swiss Alps where precipitation and humidity are both apparently higher than in the Colorado Rockies and where a permanent snow cap persists to moisten the slopes in the alpine zone, investigation has shown that the ultimate vegetation for most of the region—the Curvuletum—is rather xerophytic, and that even in regions with underlying limestone the soil reaction is distinctly acid. As to the importance of the soil reaction in determining the ultimate floristic composition of the climax meadow, the writer is in doubt, but it seems quite possible that indirectly it is a factor of importance in its relation to the maintenance of the rather general impoverished condition of the soil in the dry alpine meadow.

The ability of *Elyna bellardi* by means of its vigorous and extensive root system to assume almost complete control of the soil in its habitat means that competition for water and nutrients in the community is severe. Plants with low demands for these materials and with qualities enabling them to endure the severe exposure of the rather open habitat stand the best chance of succeeding in the meadow with the dominating Elyna. Small xerophytic species from fell field and dry meadow communities and moderately mesophytic species from the mesophytic meadow appear best adapted to such conditions. Such plants are most prominent as companion species in the Elynetum.

ALPINE SUCCESSION

The course of development of alpine vegetation has already been traced in a detailed manner from its beginning on exposed rocks through different pioneer associations of dry habitats, through dry meadow to the climax meadow; and from its beginning along stream and lake margins through various types of wet meadow and sedge moor to the climax meadow. The diagram in Figure 12 summarizes in a general way the main lines of succession as indicated by the present study.

The xerarch sere begins with species of xerophytic lichens on bare rock surfaces. Less xerophytic foliose lichens succeed these and are followed by xerophytic mosses which form small polsters. The latter sometimes serve as germinating beds for disseminules of certain pioneer humus-requiring plants. Seeds finding lodgment on polsters or in cracks and crevices of rocks germinate, and the seedlings survive for a time. Eventually accumulation of humus and erosion products results in the formation of a poor soil which makes possible the completion by pioneer species of their entire life cycle. Vegetation gradually increases on ledges, among boulders, on fell fields and slides, with resultant progress in soil development. A meadow-like vegetation is developed on stable areas of accumulated soil. This dry meadow of rather impoverished vegetation, characterized through most of its extent

by *Carex rupestris* and *Sieversia turbinata* but occasionally dominated locally for long periods of time on stony slopes by the shrub association of *Dryas octopetala*, is ultimately succeeded by the xero-mesophytic sedge meadow climax vegetation in which the leading role is taken by *Elyna bellardi*.

The hydrarch sere begins in streams and lakes or about wet stony areas or snow drifts. Hydrophytic species of flowering plants form wet meadows

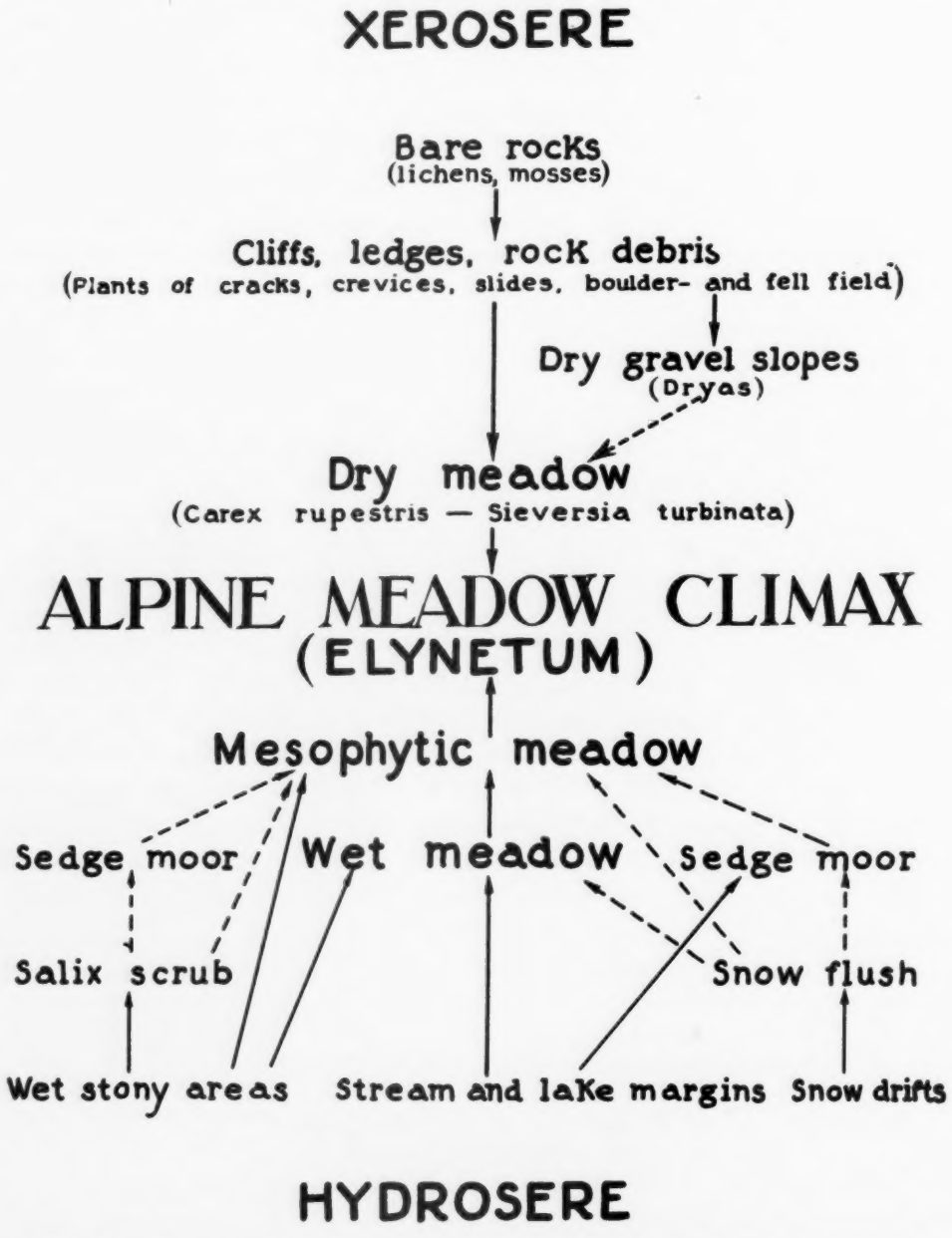

FIG. 12. Diagrammatic representation of the main lines of alpine plant succession in xero- and hydroseres. Especially long enduring locally distributed edaphic associations can be recognized by the broken lines which continue beyond them.

along stream and lake margins, or snow flush meadows where late melting snow saturates the soil during an abbreviated growing period. In places of relatively high and constant water relations sedge moors sometimes develop. Coarse wet gravels are frequently populated by willow communities, or they may also sometimes develop into sedge moors. Decreasing soil water content in any of these communities, as a result either of building up the soil level by accumulations of humus and mineral matter or of more efficient drainage, is followed by invasion by species of lower water requirements. Mesophytic meadow is the result. Still further lowering of the water content in the habitat eventually permits the entrance into the community of *Elyna bellardi* and other xero-mesophytes. These constitute the climax meadow vegetation or Elynetum which appears best suited to succeed itself indefinitely under the extreme climatic conditions of the alpine region.

ALPINE PLANTS OF JAMES PEAK

The first definite information concerning vegetation and climate of alpine altitudes in the Rocky Mountains came from botanical explorations made during the nineteenth century. As early as 1824 Torrey (1824) enumerated new or rare plants from the Rocky Mountains, and a few years later (Torrey 1828) he gave an account of plant collections which had been made by Dr. Edwin P. James during an expedition to the Rocky Mountains in the summer of 1820. Dr. Charles C. Parry (1862, 1868) made several trips into the Colorado Rockies in the decade from 1860 to 1870, collecting and enumerating many species of alpine plants, and describing physiographic and climatic conditions in the high mountain regions. Hall and Harbour accompanied Parry on his western journey in 1862 and collected many plants throughout the region.

Most of the plants brought back from the mountains passed under the careful scrutiny of such men as Torrey, Gray (1863), Englemann, and Parry in this country, and many of them were sent to Hooker and other prominent European authorities. The names of these early botanists are perpetuated alike in the names of the species and of the peaks of these high mountains. Among the names prominent on pages of Rocky Mountain floras of more recent years none appear more frequently perhaps than those of Rydberg and A. Nelson.

As has always happened in the history of the biological sciences, the rather fascinating work of collecting and identifying the species made much more rapid progress than the investigation of ecological and physiological relationships. Discussions concerning probable centers of orgin and possible lines of migration of the genera and species constituting the present Rocky Mountain flora, based upon present and past geographical distribution of these and closely related groups in the high mountains and in the arctic regions of both eastern and western hemispheres, are given by Rydberg

(1914) and Holm (1927). Publications by these two botanists give details concerning present distribution and racial affinities, so far as they are known, of many of the species occurring in the vicinity of James Peak.

The alpine vegetation of James Peak shows pronounced northern affinities. Many of the species occur in the far North where the alpine zone descends to the arctic lowland. There they frequently range clear across the continent. The study made by Holm (1927) of the geographic distribution and the floristic affinities of a number of strictly alpine species occurring on the higher Colorado peaks shows that many of the species collected on James Peak during the present investigation are circumpolar, that a considerable number occur in the Alps of central Europe, and some in the high mountains of central Asia. The following are a few of the species which are circumpolar and occur in the Alps: *Silene acaulis, Arenaria sajanensis, Stellaria longipes, Sagina saginoides, Oxyria digyna, Lloydia serotina, Polygonum viviparum, Erigeron uniflorus,* and *Luzula spicata.*

In general, circumpolar species which also occur on high mountain ranges far to the south are regarded as having originated in the arctic regions long before the glacial period, at which time they were able to migrate southward to these mountains. Upon the retreat of the ice sheet a number of species of more southern origin probably followed the melting ice and in this way became a part of the arctic flora.

Disjunct species of widely separated regions, if they have a single point of origin, as is generally believed, possibly represent species of a former extensive range which have disappeared from intervening spaces. Their probable centers of origin are usually determined by studying their geographic distribution in connection with the distribution of all closely allied groups.

Endemic species have probably originated in more recent times within their present areas. Some endemic species of common occurrence on James Peak are: *Lychnis montana, Claytonia megarrhiza, Trifolium nanum, Saxifraga chrysantha, Oreoxis alpina, Eritrichium argenteum, Chionophila jamesii, Mertensia alpina, Synthyris alpina,* and *Primula angustifolia.*

Floristic affinity studies point to four principal centers of origin for the alpine species: (1) the Rocky Mountain alpine, (2) the Arctic, (3) the European alpine, and (4) the Asiatic alpine. A number of species are believed to have moved up into the alpine zone from lower altitudes. Some of these are: *Dasiophora fruticosa, Kalmia polifolia, Arctostaphylos uva-ursi, Vaccinium oreophilum, Campanula rotundifolia, Pedicularis groenlandica,* and *Aira caespitosa.*

The alpine vegetation on James Peak may therefore be considered as made up of species (1) of Alpine origin consisting (a) of plants originating in the Rocky Mountains since the ice age, and (b) of plants from alpine regions of other continents originating before the ice age; (2) of Arctic origin preceding the ice age; and (3) of lowland origin either before or since the

glacial period. A few species, like *Pinus aristata*, have their main range south of James Peak. The latter is possibly an endemic species originating in the subalpine zone farther south.

The following list of species collected in the vicinity of James Peak includes plants reaching their uppermost limit in the wind timber of the alpine-subalpine transition belt as well as the true alpine species which are common in the region above tree limit. Consequently some of the names are not always included in lists of alpine plants. Species encountered only in the wind timber are indicated by the asterisk (*) and no attempt was made to determine their lower altitudinal limit.

One set of the collections upon which this report is based is deposited in the Herbarium of the Field Museum at Chicago; and one is retained by the writer.

ALPINE PLANTS OF JAMES PEAK

Ophioglossaceae

**Botrychium lanceolatum* (Gmel.) Augs.

Polypodiaceae

Cryptogramma acrostichoides R. Br.

**Polystichum lonchitis* (L.) Roth

Filix fragilis (L.) Gilib.

Lycopodiaceae

Lycopodium selago L.

**Lycopodium annotinum* L.

Selaginellaceae

Selaginella densa Rydb.

Selaginella underwoodii Hieron.

Pinaceae

**Pinus flexilis* James

**Pinus aristata* Engelm.

**Pinus murrayana* Balf.

**Picea engelmanni* (Parry) Engelm.

**Abies lasiocarpa* (Hook) Nutt.

**Juniperus communis sibirica* (Burgsd.) Rydb.

Gramineae

Stipa lettermanni Vasey

Phleum alpinum L.

**Agrostis hiemalis* (Walt) B. S. P.

**Calamagrostis canadensis* (Michx) Beauv.

Calamagrostis purpurascens R. Br.

Aira caespitosa L.

**Aira atropurpurea* Wahl.

Trisetum spicatum (L) Richt.

Trisetum wolfii Vasey
Avena mortoniana Scribn.
Danthonia intermedia Vasey
Poa alpina L.
Poa arida Vasey
Poa fendleriana (Steud) Vasey
Poa grayana Vasey
Poa interior Rydb.
Poa pattersoni Vasey
Poa pudica Rydb.
Poa reflexa Vasey and Scribn.
Poa rupicola Nash
Festuca brachyphylla Schult.
Festuca rubra L.
**Bromus ciliatus* L.
Agropyron scribneri Vasey
Agropyron tenerum Vasey

Cyperaceae

**Eleocharis tenuis* (Willd.) Schultes
Elyna bellardi (All) Degl.
Elyna macrocarpa Clokey ined.
**Carex aquatilis* Wahl.
Carex arapahoensis Clokey
Carex atrata L.
Carex capillaris L.
Carex capitata L.
Carex chalciolepis Holm
Carex ebenea Rydb.
Carex festiva Dewey
Carex festivella Mack.
Carex illota Bail.
Carex misandra R. Br.
Carex nigricans C. A. Meyer
Carex nova Bail.
Carex nubicola Mack.
Carex petasata Dewey
Carex phaeocephala Piper
Carex pratensis Drej.
Carex pyrenaica Wahl.
**Carex rossii* Boot.
Carex rupestris All.
Carex scopulorum Holm

Carex siccata Dewey
Carex variabilis Bail.

Juncaceae
**Luzula subcapitata* Rydb.
Luzula spicata (L.) DC.
Luzula parviflora (Ehrh.) Desv.
Juncus mertensianus Bong.
Juncus triglumis L.
Juncus castaneus Smith
Juncus parryi Engelm.

Liliaceae
Allium pikeanum Rydb.
Lloydia serotina (L.) Sweet

Melanthaceae
Zygadenus elegans Pursh

Orchidaceae
**Limnorchis stricta* (Lindl.) Rydb.
**Listera nephrophylla* Rydb.

Salicaceae
**Populus tremuloides* Michx.
Salix barclayi Anders.
Salix pseudolapponum von Seemen (*S. glaucops* And. of authors)
Salix petrophila Rydb.
Salix chlorophylla Anders.
Salix saximontana Rydb.
Salix nivalis Hooker
Salix monica Bebb. (S. planifolia monica (Bebb) Schn.)

Betulaceae
Betula glandulosa Michx.

Polygonaceae
**Eriogonum subalpinum* Greene
Eriogonum xanthum Small
Oxyria digyna (L.) Camptdera
Polygonum bistortoides Pursh.
Polygonum bistortoides lincarifolium (Wats.) Small
Polygonum viviparum L.
**Polygonum aviculare* L.
**Polygonum engelmanni* Greene

Chenopodiaceae
**Chenopodium leptophyllum* (Moq.) Nutt.
**Monolepis nuttalliana* (R. & S.) Engelm.

Portulacaceae
Claytonia megarrhiza (Gray) Parry
Lewisia pygmaea (Gray) Robins

Caryophyllaceae
Silene acaulis L.
Lychnis montana Wats.
**Lychnis drummondii* Wats.
Stellaria umbellata Turcz.
Stellaria longipes Goldie
Cerastium beeringianum Cham. & Schlect.
Cerastium arvense L.
Sagina saginoides (L.) Brit.
Arenaria aequicaulis A. Nels.
Arenaria sajanensis Willd.
Arenaria fendleri Gray
Paronychia pulvinata Gray
Ranunculaceae
Caltha rotundifolia (Huth) Greene
**Trollius albiflorus* (Gray) Rydb.
**Aquilegia coerulea* James
Aquilegia saximontana Rydb.
**Anemone globosa* Nutt.
**Pulsatilla hirsutissima* (Pursh) Brit.
Ranunculus drummondii Greene
Ranunculus alpeophilus A. Nels.
Ranunculus pedatifidus J. E. Smith
Ranunculus alismaefolius Geyer
Ranunculus adoneus Gray
Thalictrum alpinum L.
Papaveraceae
Papaver radicatum Rottb.
Cruciferae
Thlaspi coloradoense Rydb.
Thlaspi glaucum A. Nels.
**Roripa alpina* (Wats.) Rydb.
**Cardamine cordifolia* Gray
**Capsella bursa-pastoris* Medik.
Draba fladnizensis Wulf.
Draba cana Rydb.
Draba crassifolia Grahm.
Draba aurea Vahl.
Draba streptocarpa Gray
Draba chrysantha Wats.
**Arabis drummondii* Gray
**Arabis divaricarpa* A. Nels.
Erysimum nivale (Greene) Rydb.

Crassulaceae
Sedum stenopetalum Pursh
Sedum integrifolium (Raf) A. Nels.
Sedum rhodanthum Gray
Saxifragaceae
**Parnassia fimbriata* Banks, Kon. & Sims
Heuchera parvifolia Nutt.
Heuchera bracteata (Torr.) Ser.
**Mitella pentandra* Hook.
Saxifraga flagellaris Willd.
Saxifraga chrysantha Gray
Saxifraga debilis Engelm.
Saxifraga cernua L.
Saxifraga austromontana Wiegand.
Saxifraga caespitosa L.
**Saxifraga arguta* Don.
Saxifraga rhomboidea Greene
**Saxifraga austrina* A. Nels.
Grossulariaceae
**Ribes montigenum* McClatchie
**Ribes coloradoense* Coville
**Ribes lacustre* (Pers.) Poir
Rosaceae
Dryas octopetala L.
**Rubus strigosus* Michx. (R. melanopsis Focke)
Dasiophora fruticosa (L.) Rydb.
Sibbaldia procumbens L.
**Fragaria ovalis* (Lehm.) Rydb.
Potentilla crinita Gray
Potentilla nelsoniana Rydb.
Potentilla quinquefolia Rydb.
Potentilla nivea L.
Potentilla uniflora Ledeb.
Potentilla glaucophylla Lehm.
Potentilla saximontana Rydb.
Potentilla diversifolia Lehm.
Sieversia turbinata (Rydb.) Greene
Leguminosae
Trifolium nanum Torr.
Trifolium parryi Gray
Trifolium dasyphyllum T. & G.
Violaceae
Viola biflora L.

Viola bellidifolia Greene
**Viola blanda Willd.*
Onagraceae
Chamaenerion latifolium L.
Chamaenerion angustifolium (L.) Scop.
Epilobium lactiflorum Haussk.
Umbelliferae
Oreoxis alpina (Gray) C. & R.
**Angelica grayi* C. & R.
Pseudocymopterus montanus (Gray) C. & R.
Pyrolaceae
**Pyrola secunda* L.
**Pyrola minor* L.
**Moneses uniflora* (L.) Gray
Ericaceae
**Kalmia polifolia* Wang.
**Gaultheria humifusa* (Graham) Rydb.
**Arctostaphylos uva-ursi* (L.) Spreng.
Vacciniaceae
Vaccinium oreophilum Rydb.
**Vaccinium caespitosum* Michx.
Primulaceae
Primula angustifolia Torr.
Primula parryi Gray
Androsace subumbellata A. Nels.
Gentianaceae
Chondrophylla americana (Engelm.) A. Nels.
Gentiana monantha A. Nels.
**Gentiana plebeja* Cham.
Gentiana plebeja holmii Wettst.
Gentiana romanzovii Ledeb.
**Gentiana parryi* Engelm.
Swertia palustris A. Nels.
Swertia congesta A. Nels.
Frasera speciosa Griseb.
Polemoniaceae
Phlox caespitosa var. *condensata* (Gray) E. Nels.
**Polemonium pulcherrimum* Hook.
Polemonium confertum Gray
Hydrophyllaceae
Phacelia sericea (Graham) Gray
Boraginaceae
**Lappula* sp.

Eritrichium argenteum Wight.
Mertensia alpina (Torr.) Don
Mertensia bakeri lateriflora (Greene) A. Nels.
Mertensia ovata Rydb.
Mertensia ciliata (Torr.) Don

Scrophulariaceae
**Penstemon glaucus stenosepalus* Gray
**Penstemon alpinus* Torr.
Chionophila jamesii Benth.
Synthyris alpina Gray
Veronica alpina L.
**Veronica serpyllifolia* L.
**Pedicularis racemosa* Dougl.
Pedicularis grayi A. Nels.
Pedicularis parryi Gray
Pedicularis scopulorum Gray
Pedicularis groenlandica Retz.
Castilleja brachyantha Rydb.
Castilleja occidentalis Torr.
**Castilleja lauta* A. Nels.
Castilleja rhexifolia Rydb.

Caprifoliaceae
**Sambucus microbotrys* Rydb.

Adoxaceae
**Adoxa moschatellina* L.

Campanulaceae
Campanula uniflora L.
Campanula rotundifolia L.

Valerianaceae
**Valeriana edulis* Nutt.
Valeriana acutiloba Rydb.

Compositae
**Chrysopsis pumila* Greene
Tonestus pygmaeus (T. & G.) A. Nels.
Tonestus lyallii (Gray) A. Nels.
Solidago decumbens Greene
**Aster apricus* (Gray) Rydb.
Aster culminus A. Nels.
Machaeranthera pattersonii (Gray) Greene
Erigeron salsuginosus Gray
Erigeron salsuginosus var. *glacialis* (Nutt.) Gray
**Erigeron elatior* (Gray) Greene
**Erigeron superbus* Greene

Erigeron melanocephalus A. Nels.
Erigeron uniflorus L.
**Erigeron leiomeris* Gray
Erigeron debilis (Gray) Rydb.
**Erigeron compositus* Pursh
**Erigeron compositus discoideus* Gray
Antennaria parvifolia Nutt.
**Antennaria rosea* (Eat.) Greene
Antennaria concinna A. Nels.
Antennaria aprica Greene
**Antennaria pulcherrima* (Hook.) Greene
**Anaphalis subalpina* (Gray) Rydb.
Chaenactis alpina (Gray) Jones
Actinea lanata (Nutt.) Kuntze
Rydbergia grandiflora (Pursh) Greene
Achillea subalpina Greene
Artemisia borealis Pall.
Artemisia scopulorum Gray
Artemisia pattersonii Gray
Artemisia saxicola Rydb.
**Arnica cordifolia* Hook.
**Arnica pumila* Rydb.
**Arnica ventorum* Greene
**Arnica subplumosa* Greene
**Arnica rydbergii* Greene
**Arnica parryi* A. Gray
**Senecio kuntzei* Rydb.
**Senecio purshianus* Nutt.
**Senecio amplectens* A. Gray
Senecio holmii Greene
Senecio taraxacoides (Gray) Greene
Senecio carthamoides Greene
**Senecio triangularis* Hook.
**Senecio crassulus* Gray
Senecio atratus Greene
**Senecio werneriaefolius* Gray
Senecio petrocallis Greene
**Senecio fendleri* Gray
Senecio crocatus Rydb.
Carduus sp.
Crepis sp.
Hieracium gracile Hook.
**Agoseris glauca* (Nutt.) Greene

**Agoseris aurantiaca* (Hook.) Greene
**Agoseris purpurea* (Gray) Greene
Taraxacum scopulorum (Gray) Rydb.
**Taraxacum mexicanum* DC.
Taraxacum ceratophorum (Ledeb.) DC.

DISCUSSION

Regions of moderate altitude and latitude usually lie well within limits of temperature and growing season critical for species constituting their vegetation. Consequently these factors are of minor importance in determining the species present. Soil moisture frequently assumes first place in such locations, and other environmental factors rank about in accord with their effect upon soil moisture relations. Under conditions of moderate rainfall and low humidity which obtain during summer on the prairie, Weaver (1931) finds soil moisture and humidity most important in controlling floristic composition.

On the vegetation frontier in the alpine zone both rainfall and humidity are relatively high. Here, where growing season and temperature are near their limit for plant life, these factors assume first rank in determining the species which constitute the vegetation. In a region of such rigid conditions for plant life it seems probable that any factor having much effect upon the environment may prove at times to be limiting for the existence of particular species. Regardless of how favorable other environmental conditions may be, the short growing season limits decidedly the number of species which can persist at this high altitude. No such sweeping statement may be made in regard to temperature. Many species can tolerate even lower temperatures than occur in any part of the alpine zone. Still, temperature does set the upper limit for a number of alpine plants, though less frequently perhaps than does the brief growing season. Due to persistence of snow drifts or to low light intensity the growing period is so short that certain places support no vegetation at all, and on large areas the best vegetation possible is very meager.

It must not be thought, however, that soil moisture is unimportant in alpine habitats. A consideration of conditions existing in various plant communities furnishes convincing evidence to the contrary. In the distribution within these communities of the species which are able to complete their life cycles during the few weeks of growing weather, in spite of frosts which may occur at any time, the water relations existing in the various habitats appear more often than any other single factor to be controlling. This fact is brought out in a prominent way in the study of alpine plant succession.

In regard to factors important in the distribution of species at high altitudes it might be said in general that temperature and length of growing

season are of primary importance in controlling the vertical distribution while soil moisture is probably first in determining the horizontal distribution into various habitats at any given level. Of course the term "level" is used in a broad sense, as length of growing season and temperature rarely, if ever, vary consistently with altitude. The longest persisting snow drifts frequently lie well down in the alpine zone. Cold air flows down and late frosts frequently occur in narrow valleys or ravines far below the mountain summits. It has already been noted that late frosts and short growing season, in combination with the desiccating effect of winds at times when soil water is deficient, are important in fixing the upper limit of tree species below that of herbaceous plants. To a somewhat more limited degree these same factors working together set the upper limits of many herbaceous species. A considerable number of herbaceous plants, however, may be found growing at any altitude in the alpine zone restricted of course to their particular habitat. Soil moisture relations more often than any other condition impose this restriction. In other words, temperature and growing season sometimes become of minor consideration in the distribution of alpine species.

The strong wind affects the water relations within the plant by decreasing soil water as a result of accelerated evaporation rate and by increasing transpiration rate. Dead branches and deformed trees of wind timber, patches of dead vegetation on windswept slopes, and strict zonation of species according to degree of wind exposure constitute evidence of the important role of wind in determining the alpine species and their distribution. Erosion, distribution of soil, pollination, and seed dispersal are other important activities performed by wind.

Precipitation and humidity are both relatively high, but both undergo considerable fluctuation during the growing season. During periods with little rainfall, strong wind, and bright sunlight, humidity and soil water are both reduced at a time when the evaporation rate is high. Only in stream or lake margin communities or in mesic habitats where exposure is less severe can plants of high water requirements survive. Even in such places the water supply may be reduced temporarily, and soil moisture may sink below the limit necessary for survival of certain species.

Snow is of value as a protection during winter for certain species as well as for its conserving effect upon the moisture supply for the summer. On the other hand, there are the snow avoiding species which occur only where snow does not accumulate. Wind is quite important in connection with the disposition of snow cover. While light has an important influence both in relation to photosynthetic activity and in its effect upon evaporation rate, it appears that the majority of the species have light requirements well within the extreme limits of light intensity of the region.

Alpine soils are in general rather consistently nutrient-poor, acid in reaction, and immature in development. Most alpine species appear to have a

considerable range of soil tolerance. The most immediate effect arising from differences in the amount of humus present in various habitats is probably the resulting difference in water holding capacity of the soil.

It seems, therefore, that in the distribution of alpine species throughout the region, length of growing season, temperature, and soil moisture relations probably play the leading role; wind, evaporation, precipitation, humidity, light, and soil, except in extreme cases, are to be regarded as of secondary importance. Furthermore the dwarfed condition of the vegetation appears to result from the brief growing period and from deficient water relations within the plant due to frequent low soil temperatures and occasional rainless periods with high evaporation rates. Intense light and poor soil contribute to this stunted condition. In exposed positions high wind affects the growth mechanically as well as physically. Biotic factors, with the exception of forest fires, which have sometimes brought about the downward extension of alpine conditions and vegetation beyond the former alpine-subalpine border, appear to have had little influence upon the vegetation.

In tracing the course of development of alpine vegetation it appears that in both hydrosere and xerosere, so long as one deals with areas in which the growing season is sufficient for progressive development by the vegetation, the primary influence in bringing about the successional development is changing conditions in soil moisture. These changes in habitat are necessarily accompanied by changes in the floristic composition of the plant community. Associations appear, develop to maturity, and gradually give way to new ones, probably more in response to changing water relations in the habitat than to other conditions although other factors must constantly be considered. Floristic studies made in the same type of community at different altitude and exposure show some differences, of course, in species present; but in general there is considerable uniformity in the dominants and the characteristic species.

The lines of development as indicated by floristic changes point to a gradual convergence towards a fairly uniform meadow vegetation which appears where the soil becomes fairly well developed and as nearly stabilized by vegetation as the severe climate and strong relief of the region will permit. The vegetation has reached this climax stage of development on broad gentle slopes and on small isolated areas in the more stable situations. The characteristic species of the climax association, the Elynetum, must be more or less xerophytic in order to succeed under the rather rigid conditions for plant development which prevail on the high mountain slopes.

Parts of the region, where the vegetation is prevented by long-enduring local conditions in the soil from progressing noticeably towards the climax stage for extremely long periods of time and where characteristic and distinctive plant communities persist, support edaphic climax types or associations. Ultimately these areas too appear to yield to the combined in-

fluence of climate and vegetation and are invaded by the species from the climax meadow.

SUMMARY

1. Environmental conditions and vegetation were studied in the alpine zone on James Peak during the growing seasons of 1928 and 1929.

2. Alpine climate approaches that of the arctic in severity. The growing season varies from three to twelve weeks. The daily temperature range during summer is excessive. The days are moderate to warm, but frost may occur almost any night. Growing season, temperature, and soil moisture are of first importance in determining species present, their distribution, and the dwarfed condition of the plants.

3. Light intensity is high and is connected with the reduced size of plants and modified leaf structure. Light accelerates evaporation and affects the distribution of species.

4. The total precipitation and the humidity are relatively high but undergo considerable fluctuation during the growing season. Most of the precipitation occurs in the form of snow during the resting period of the plants. Snow serves as winter protection for certain species and conserves some of the winter precipitation for use during the summer. Run off is high.

5. Strong winds are characteristic of alpine climate. Wind influences the disposition of winter snow, accelerates evaporation, reduces soil moisture content, and exerts a very pronounced effect upon the vegetation as shown by wind timber and fell field communities.

6. Daily evaporation rates become excessive during rainless periods in summer when humidity is low. Conditions at such times are critical for vegetation.

7. Biotic factors have probably had little influence upon the vegetation.

8. Alpine vegetation consists of scrub forest, grassland, and desert.

9. Alpine scrub occupies the alpine-subalpine transition zone and consists of deformed tree species which offer protection to communities of intermingling alpine and subalpine plants.

10. Alpine desert includes sparsely populated communities of pioneer species of the rocks, of slides, and of areas where late-lying snow or low light intensity permit the development of little or no vegetation. Fell field and boulder field communities in advanced stages represent the best developed vegetation of the alpine desert. Dicotyledonous herbs dominate and constitute the principal members of these pioneer communities.

11. Alpine grassland constitutes the larger portion of the vegetation of the alpine zone and includes several rather distinct types of alpine meadow which owe their differences in floristic composition primarily to differences in soil moisture relations. Scrub associations dominated by Dryas on exposed

stony slopes and by species of Salix on wet gravels frequently interrupt the continuity of the alpine meadow.

12. In the development of the vegetation cycle the xerosere begins on the rocks. Lichen-moss associations of bare rock surfaces are succeeded by pioneer communities of cracks, crevices, and accumulated rock waste. Dry meadows, or sometimes scrub associations, develop and are eventually followed by the climax sedge meadow, Elynetum.

13. The hydrosere begins along stream and lake margins where wet meadows or sometimes moor communities composed of hydrophytes develop. Gradual and progressive decrease in soil moisture content eventually leads to invasion of these communities by species of lower moisture requirements. Mesophytic and ultimately climax meadow, Elynetum, follow.

14. Long enduring conditions at any of these stages may result in fairly well defined edaphic climax associations.

15. Most of the alpine species range far to the north of Colorado. A considerable number occur in the arctic where they are circumpolar. Some species found on James Peak occur on the high mountains of central Europe and Asia.

16. The alpine flora consists of endemic species which have probably originated in the Rocky Mountains, of disjunct species, some of which have probably originated in the arctic and some in high mountains of Europe or Asia, and of species concerning which the center of origin is doubtful since they have a continuous range over alpine and arctic regions in both eastern and western hemispheres.

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STUDIES ON THE ECOLOGICAL RELATIONS OF BEES IN THE CHICAGO REGION

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A Part of a Dissertation Submitted to the Faculty of the Division of the Biological Sciences in Candidacy for the Degree of Doctor of Philosophy

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STUDIES ON THE ECOLOGICAL RELATIONS OF BEES IN THE CHICAGO REGION

I. INTRODUCTION

The data reported in this work were accumulated as part of a program involving the eventual development of a detailed knowledge of the ecology and taxonomy of the American species of bees.[1] The attempt has been made to become acquainted with a majority of the species found within a radius of seventy-five miles of Chicago and to determine whether these species show a general adaptation to certain regions possessing various combinations of physical conditions which may be described as plant communities, and whether such adaptations, if they exist, can be demonstrated experimentally.

Cowles (1901) and his followers (Fuller 1914, 1925; etc.) have worked out the plant communities of the Chicago area and have made various studies of the physical conditions prevailing in these communities and responsible for them. Shelford in "Animal Communities of Temperate America" (1913) and more recently Holmquist (1926) and Park (1930) have studied certain animals living in these areas and have found that they form communities which, in many cases, correspond remarkably well with the plant communities not only in geographical distribution but also in succession. These workers with animal species have also devoted much time to the study and measurement of the physical factors which may be considered as exerting a limiting or controlling effect upon the distribution of the animal species, but they have by no means overlooked direct influences exerted by the plants themselves in setting up the bounds of occurrence, or possibly we should say degree of abundance, of any given species or group of animals.

Land studies have been mostly concerned with such factors as light (Park, 1930), heat, evaporation-rate and humidity (Fuller, 1914). Among all publications reporting comparative studies in the distribution of animal groups among neighboring plant communities having quite different biotic and physical make-ups, the writer is unaware of any dealing with bees, aside from some references by Cockerell (1893) to vertical distribution of bee species in a mountainous locality in Colorado, and the recent work of Graenicher (1930) dealing with bees and plant communities in the Miami, Florida, region. Shelford (1913) includes long lists of animal species taken in various communities but mentions very few species of bees.

The omission of this large group of insects from studies hitherto made can be explained but is surprising. Bees are not rare in the Chicago region,

[1] Essential portions of thesis accepted by Department of Zoölogy, University of Chicago. Acknowledgment is made of the advice and assistance of Dr. W. C. Allee, Dr. A. E. Emerson, and Dr. G. D. Fuller, of the University of Chicago, of Dr. Charles Robertson, of Carlinville, Illinois, and of Dr. T. H. Frison, of the Illinois State Natural History Survey.

nor in any region in the United States. Graenicher's list reveals Southern Florida as possessing one of the poorest of bee faunas. He gives 65 species. Viereck (1916) gives 171 species taken from Connecticut and a total of 234 to be expected there. Leonard in "Insects of New York" (1926) gives 189 species; Graenicher (1911) gives 166 species collected during two trips into Northern Wisconsin; while Robertson (1928) reports 297 species from the Carlinville, Illinois, region. The present work includes 169 named species while a considerable number await final identification or description. Any collecting for general insects made during spring, summer, or early fall, reveals bee visitors to almost every flower. Many bees are very active and hard to take and, once collected, they form one of the most difficult groups to identify to species. They have therefore suffered when named lists have been published.

Concerning the desirability of including them in descriptive lists of the constituents of various communities or regions, reference need only be made to the oligotropic relations existing between many bee species and flower species or groups, which link up irrevocably the female of the species with the community or communities in which its host plant or plants (from which alone pollen is collected), are found. Robertson (1926) presented a revised list of oligoleges from the Carlinville area. In Appendix A, a list is presented which is based on Robertson's bees and includes records of the presence of the various species in the Chicago region, along with any records of pollen collecting in the latter region. As explained in the appendix, all Chicago records are the writer's.

II. PARTIAL ECOLOGICAL CHECK-LIST OF THE BEES OF THE CHICAGO AREA

A. Requirements That Must Be Met by a Complete Check-List

Because of the close interdependence between bees and flowers (Robertson, 1895a), a complete ecological check-list of the bees of this area should give the following data:

1. Flowers on which the bee has been taken should be recorded, with the bee's sex, behavior, and abundance at different times of the day and during different periods of the blooming season for the flower species. Weather conditions should also be reported with each record.

2. The plant community in which the particular flower under consideration is growing should also be given and its general physical factors should be carried over into the summarized data for the bee species.

3. The seasonal flight for each species should be averaged over a period of several years, not merely extended by "records."

4. Consideration of abundance of visits to various flowers of various communities should permit the indication of a "preferred" community or

assembly, and perhaps a given set of physical conditions can then be indicated as "most suitable" for the species involved.

5. Nesting localities should be compared with data concerning flower visits to corroborate or offset such conclusions as may have been drawn from these data.

6. The information should be presented for all species of the area.

Accumulating such data for the bee fauna of the Chicago area would require that trips be made weekly or oftener to every major community and to many minor ones, and that every blooming plant known to have, or suspected of having, bee visitors should be watched for a period of at least half an hour, two or three different times during the day. This procedure would have to be repeated annually until the number of added species each year indicated mathematically the collection of approximately all species of the area. It would also involve careful observation of each bee before collecting it, with an almost constant recording of physical conditions of temperature, light, wind, and humidity. It would practically prevent the accumulation of any considerable number of specimens and would require almost constant work by one person during a considerable number of years.

B. Work Done Toward a Check-List

Because of the desirability of collecting as many different species of bees as possible in two years, and because of the necessity of collecting numbers of presumably the same species, the present work cannot present anything like a complete ecological check-list as described above. During the season of 1930, emphasis was placed on collecting numbers of individuals of the same species for experimental study. During a season of less intense collecting in 1931, emphasis was placed on collecting numbers of species for comparison with other regions, particularly the Carlinville area. As a result, the following list of bee species is far from complete. Little collecting was done in the dune regions, the main localities being Palos, Matteson, Lemont, and Ashburn, Illinois. Bees are, however, included from Somonauk, Waukegan, Zion, New Lenox, South Chicago, Willow Springs, Chicago, and Volo, Illinois, and Valparaiso, Tremont, and Dune Park, Indiana, as well as from other scattered localities. Collecting has been primarily in red-white oak (semi-climax), flood-plain, and prairie communities. There has been no hesitancy in collecting from ruderals and garden weeds nor from introduced or cultivated plants.

Where flower data are available or have been translated from the records, they have been included.

C. Scheme of Classification Followed

The general classification given below is a modification of Robertson (1904a). In the bumblebees, Frison (1919) has been followed. Two divergent stocks of bees are indicated.

I. Dasygastrae, Megachilidae, Stelididae.

II. Scopulipedes, Andrenidae, Nomadidae, Colletidae, Nomiidae, Prosopididae, Halictidae, Dufoureidae, Macropididae, Panurgidae, Ceratinidae, Euceridae, Emphoridae, Anthophoridae, Melectidae, Epeolidae, Pasitidae, Bombidae, Apidae.

The general arrangement of the bees has been a subject of endless dispute and little is to be gained by entering into details. Changes in opinion by the same individual indicate the instability of the general classification and the two following quotations from Robertson indicate the fact that any worker in the field of bee taxonomy must be ready to readjust his opinions as he has done.

From Robertson (1899, page 340):

To give Psithyrus this rank, I think, involves a great systematic error only equalled in the old physiological classification of Schuckard. The latter author calls those bees which carry pollen on their legs scopulipedes; those with abdominal brushes, dasygasters.

From Robertson (1924):

As far as I can infer from the local species, I do not think they (Dasygastrae) have arisen from the other bees, but that they should be separated as one of two principal groups, Dasygastrae and Scopulipedes, with the latter divided into Apygidialia and Pygidialia.

This paper follows Robertson in considering these now as two separate groups.

D. Partial Check-List of Bees of the Chicago Area, With Certain Ecological Notes

The following list represents the results of 98 field trips distributed throughout two flower seasons, during which over 6,700 bees (exclusive of specimens of *Apis mellifera*), were brought in for experimental material or observed at work.[2]

The name in current usage, with author, is given first. Numbers of specimens collected in the Chicago region are then given, followed by ecological notes in certain cases, and then by a reference to the original description or to some vital citation of the species. Flower genera cited are representative only and no attempt is made to give more than one or two field sources for

[2] Since this work was completed, further collecting and identification of bees from the Chicago Region has added the following species:

Epeolus interruptus Robt.
Epeolus lectoides Robt.
Triepeolus concavus (Cresson)
Melissodes vernoniae Robt.
Hoplitis cylindricus (Cresson)
Dianthidium notatum (Latreille)
Microstelis lateralis (Cresson)
Andrena erythrogastra (Ashmead)
Andrena geranii Robt.
Andrena mandibularis Robt.
Andrena milwaukeensis Graenicher
Andrena tridens Robt.
Andrena vicina Smith
Opandrena personata (Robt.)
Pterandrena asteris (Robt.)
Trachandrena rugosa (Robt.)
Trachandrena spireana (Robt.)
Pseudopanurgus asteris (Robt.)
Verbenapis verbenae Cockerell

the bee species. Among the Bremidae, Frison's names are given first, followed by Robertson's if they differ, the latter being in brackets.

ANTHOPHORIDAE

Amegilla walshii (Cresson) (1 ♀), August 5, Vernonia.

Anthophora Walshii Cresson (1869a) p. 290.

Anthemocssa abrupta (Say) (30 ♀ 17 ♂), Pentstemon, ♀ June 26-July 8, ♂ June 20-July 2.

Anthophora abrupta Say (1837) p. 409.

Clisodon terminalis (Cresson) (55 ♀ 25 ♂), Pentstemon, ♀ June 20-September 7, ♂ June 24-August 4.

Anthophora terminalis Cresson, (1869a) p. 292.

APIDAE

Apis mellifera Linnaeus (many workers), all localities, all available flight weather.

Apis mellifera Linnaeus (1758).

BREMIDAE (flight appearance: ♀ wintered over, workers, males, females which will winter over).

Bremus affinus (Cresson) (1 ♀ 2 workers), ♂ June, workers August, Northeastern Illinois.

Bombus affinus Cresson (1864).

Bremus americanorum (Fabricius) [*Bombus americanorum* (Fabr.)] (68 ♀ 10 ♂ 112 workers), (1930 data—17 ♀ May, 39 June, 17 July; 1 ♂ July, 3 August, 5 September, 4 October; 31 workers July, 73 August, 7 September, 2 October).

Apis americanorum Fabricius (1775) p. 380.

Bremus auricomus (Robertson) [*Bombias auricomus* Robertson] (10 ♀ 27 workers), (1930 data—1 ♀ May, 6 June, 2 July, 2 August; 19 workers July, 11 August, 3 September).

Bombias auricomus Robertson (1903c) pp. 176, 177.

Bremus bimaculatus (Cresson) [*Bombus ridingsii* Cresson] (8 ♀ 1 ♂ worker), (1930 data—3 ♀ April, 5 May; 1 ♂ July; 1 worker July).

Bombus bimaculatus Cresson (1863) [*Bombus Ridingsii* Cresson (1878) p. 182].

Bremus borealis (Kirby) (2 workers), (1930 data—1 worker July, 1 August), Northeastern Illinois.

Bombus borealis Kirby (1837).

Bremus fervidus (Fabricius) 8 ♀ 11 ♂ 50 workers), (1930 data—1 ♀ April, 4 May, 3 June; 2 ♂ July, 8 August, 1 September; 11 workers July, 38 August, 1 September, 1 October).

Apis fervida Fabricius (1798) p. 274.

Bremus fervidus dorsalis (Cresson) (2♂ 1 worker), (2 ♂ August, 1 worker August).

Bombus fervidus var. dorsalis Cresson (1879a) p. 230.

Bremus impatiens (Cresson) [*Bombus impatiens* Harris] (10 ♀ 3 ♂ 35 workers), (1930 data—7 ♀ May, 3 June; 1 ♂ September, 2 October; 1 worker July, 30 August, 3 September).

Apis virginicus Olivier (1789) [*Bombus impatiens* Cresson (1864)].

Bremus rufocinctus (Cresson) (1 ♀ August; 2 workers August), Northeastern Illinois.

Bombus rufocinctus Cresson (1863).

Bremus rufocinctus albertensis (Cockerell) (2 workers August), Northeastern Illinois.

Bombus hyperboreus var. albertensis Cockerell (1909).

Bremus separatus (Cresson) [*Bombias separatus* (Cresson)] (14 ♀ 10 ♂ 49 workers), (1930 data—1 ♀ April, 2 May, 7 June, 2 July, 2 August; 7 ♂ August, 2 October; 17 workers July, 30 August, 2 September) Prairie.

Bombus separatus Cresson (1864).

Bremus vagans (F. Smith) [*Bombus consimilis* Cresson] (28 ♀ 7 ♂ 178 workers), (2 ♀ May, 20 June, 6 July, 1 August; 1 ♂ July, 5 August, 1 October; 57 workers July, 120 August, 2 October).

Bombus vagans Smith (1854) p. 399 [*Bombus consimilis* Cresson (1864)].

Psithyrus laboriosus (Fabricius) (5 ♀ 3 ♂), (♀ June, 4 July; 3 ♂ August).

Bombus laboriosus Fabricius (1804) p. 352.

Psithyrus variabilis (Cresson) (5 ♂), (2 August, 1 September, 2 October).

Apathus variabilis Cresson (1872) p. 284.

CERATINIDAE

Ceratina dupla Say (190 ♀ mixed with next two, 31 ♂), ♀ April 11-October 10; ♂ April 12-September 13, widespread, numerous.

Ceratina dupla Say (1837) p. 397.

Zaodontomerus calcaratus (Robertson) (3 ♀ and others mixed with *C. dupla*, 1 ♂), all August 5, Tithymalopsis, oak dunes.

Ceratina tejonensis Cresson (1864).

Zaodontomerus metallica (Smith) (♀ mixed with *C. dupla*, 4 ♂) ♀ April 11-October 10; ♂ June 14-September 7.

Ceratina metallica Smith, H. S. (1907).

EPEOLIDAE

Epeolus autumnalis Robertson (1 ♀ August 30).

Epeolus autumnalis Robertson (1902a) p. 81.

Epeolus pusillus Cresson (1 ♀ 4 ♂), ♀ August 22, *Rudbeckia hirta*.

Epeolus pusillus Cresson (1864).

Triepeolus cressonii (Robertson) (1 ♀ August 23) Vernonia.

Epeolus cressonii Robertson (1897) p. 344.

Triepeolus donatus (Smith, F.) (♀ 16 ♂ 13), ♀ August 9-26; ♂ August 12-26, Cirsium, prairie.

Epeolus donatus Smith (1854) p. 256.

Triepeolus helianthi (Robertson) (1 ♀ 1 ♂), ♀ August 5; ♂ July 4, *Helianthus divaricatus*.

Epeolus helianthi Robertson (1897) p. 344.

Triepeolus pectoralis (Robertson) (♀ 2), August 30, Vernonia.

Epeolus pectoralis Robertson (1897) p. 345.

Triepeolus simplex Robertson (3 ♀), August 1-22, *Helenium autumnale, Helianthus divaricatus*.

Triepeolus simplex Robertson (1903b) p. 285.

EUCERIDAE

Epimelissodes obliqua (Say) (7 ♀ 2 ♂), ♀ July 15-August 5; ♂ August 14-23; Helenium, Helianthus.

Macrocera obliqua Say (1837) p. 403.

Melissodes agilis Cresson (13 ♀ 142 ♂), ♀ July 11-September 2; ♂ July 11-September 2, Helianthus and many fall composites.

Melissodes agilis Cresson (1878) p. 204.

Melissodes bimaculata (LePelétier) (♀ 10 ♂ 12), ♀ June 5-September 13; ♂ July 2-August 26, Monarda.

Macrocera bimaculata LePelétier (1825) p. 527.

Melissodes boltoniae Robertson (possibly many of each sex, ♀ mixed with *M. vernoniana*, ♂ mixed with *M. simillima*, not clearly definable).

Melissodes boltoniae Robertson (1905a) p. 368.

Melissodes cnici Robertson (25 ♀ 51 ♂), ♀ August 9-September 5; ♂ July 11-August 26, Cirsium.
Melissodes cnici Robertson (1901) p. 230.
Melissodes coloradensis Cresson (6 ♀), August 30-September 5, Helianthus.
Melissodes coloradensis Cresson (1878) p. 200.
Melissodes nivea Robertson (8 ♂), August 5-23, Helianthus.
Melissodes nivea Robertson (1895b) p. 127.
Melissodes simillima Robertson (15 ♀, ♂ mixed with *M. boltoniae*, 75 or more if all *simillima*), ♀ August 23-October 4; ♂ June 27-August 30, *Verbena stricta*, Vernonia.
Melissodes simillima Robertson (1897) p. 355.
Melissodes trinodis Robertson (33 ♀ 92 ♂), ♀ July 2-September 7; ♂ July 11-September 5, Rudbeckia Helianthus, Verbena.
Melissodes trinodis Robertson (1901) p. 231.
Melissodes vernoniana Robertson (♀ mixed with *M. boltoniae*, 115 if all *vernoniana*; ♂ 18), ♀ June 27-September 12; ♂ June 27-July 19, Vernonia, Verbena.
Melissodes vernoniana Robertson (1905a) p. 368.
Tetralonia dilecta (Cresson) (12 ♀), June 20-July 6, Rosa, Pentstemon.
Melissodes dilecta Cresson (1878) p. 199.
Tetralonia rosae (Robertson) (9 ♀ 5 ♂), ♀ June 14-20; ♂ June 14.
Synhalonia rosae Robertson (1900) p. 54.
MEGACHILIDAE
Alcidamea simplex (Cresson) (60 ♀ 2 ♂), ♀ June 14-July 6; ♂ June 14, Pentstemon.
Heriades simplex Cresson (1864).
Alcidamea truncata Cresson (9 ♀ 2 ♂), ♀ June 21-28; ♂ June 14.
Alcidamea truncata Cresson (1878a) p. 108.
Ceratosmia lignaria (Say) (4 ♂), April 12-19, Claytonia.
Osmia lignaria Say (1837) p. 399.
Gnathosmia georgica (Cresson) (2 ♀ June 14 and 20) Pentstemon.
Osmia georgica Cresson (1878a) p. 105.
Monilosmia canadensis (Cresson) (10 ♀), June 20-28, Pentstemon.
Osmia canadensis Cresson (1864).
Osmia atriventris Cresson (7 ♀), June 14-July 2, Pentstemon.
Osmia atriventris Cresson (1864).
Osmia collinsiae Robertson (2 ♀ June 20 and 28), Pentstemon.
Osmia major Robertson (1902a) p. 79.
Osmia distincta Cresson (85 ♀), June 14-July 26, Pentstemon.
Osmia distincta Cresson (1864).
Osmia pumilia Cresson (42 ♀ 13 ♂), ♀ May 10-June 28; ♂ April 11-May 10, Pentstemon.
Osmia pumila Cresson (1864).
Neotrypetes barbatus (Robertson) (20 ♀ 3 ♂), ♀ July 8-29; ♂ June 4-5, Monarda.
Trypetes barbatus Robertson (1903c) p. 171.
Neotrypetes productus (Robertson) (10 ♀ 2 ♂), ♀ June 28-July 28; ♂ June 14, Erigeron.
Trypetes productus Robertson (1905) p. 236.
Anthemois centuncularis (Linnaeus) (3 ♀ 6 ♂), ♀ July 10-August 23; ♂ July 10-August 23.
Apis centuncularis Linnaeus (1766-8).
Cyphopyga montivaga (Cresson) (9 ♀ 6 ♂), ♀ June 14-August 26; ♂ June 24-August 23, Pentstemon.

Megachile montivaga Cresson (1878a) p. 124.

Megachile brevis Say (11 ♀ 15 ♂), ♀ July 6-September 11; ♂ June 20-September 11, widespread, numerous.

Megachile brevis Say (1837) p. 407.

Megachile generosa Cresson (1 ♀ 1 ♂), ♀ June 24; ♂ July 19, Verbena, *Monarda punctata*.

Megachile generosa Cresson (1878a) p. 125.

Megachile mendica Cresson (9 ♀ 15 ♂), ♀ June 27-September 5; ♂ July 2-August 27, Helenium, Rudbeckia.

Megachile mendica Cresson (1878a) p. 126.

Megachile petulans Cresson (39 ♀ 1 ♂), ♀ July 4-August 19; ♂ July 30, Vernonia, Pentstemon.

Megachile petulans Cresson (1878a) p. 127.

Oligotropus campanulae Robertson, (2 ♀ 7 ♂), ♀ July 25-26; ♂ June 25-July 25, *Campanula americana*.

Oligotropus campanulae Robertson (1903c).

Sayapis pugnata (Say) (16 ♀ 4♂), ♀ July 2-August 2; ♂ July 2-July 15, Silphium, Vernonia.

Megachile pugnata Say (1837) p. 408.

Sayapis sayi (Cresson) (29 ♀ 9 ♂), ♀ July 11-September 11; ♂ July 30-August 30, Lepachys.

Megachile Sayi Cresson (1878a) p. 119.

Xanthosarus latimanus (Say) (65 ♀ 16 ♂), ♀ June 24-September 20; ♂ June 27-August 23, Vernonia, Rudbeckia, and other Composites.

Megachile latimanus Say (1859) p. 169.

Coelioxys alternata Say (4 ♀ 1 ♂), ♀ July 11-September 11; ♂ July 30, Verbena.

Coelioxys alternata Say (1837) p. 401.

Coelioxys germana Cresson (2 ♀), August 5 and 6, Helianthus.

Coelioxys germana Cresson (1878a) p. 102.

Coelioxys modesta Smith (2 ♀ 1 ♂), ♀ August 30; ♂ July 4, Verbena, Pentstemon.

Coelioxys modesta Smith (1854) p. 271.

Coelioxys octodentata Say (2 ♂), July 6-August 19, Melilotus.

Coelioxys octodentata Say (1859).

Coelioxys rufitarsis Smith (2 ♀), July 25-August 23, Solidago, Helianthus.

Coelioxys rufitarsis Smith, F. (1854) p. 271.

Coelioxys sayi Robertson (5 ♀ 9 ♂), ♀ June 28-August 30; ♂ July 31-August 9, Helianthus, Verbena.

Coelioxys sayi Robertson (1897) p. 346.

NOMADIDAE

Centrias americanus (Kirby) (11 ♀ 8 ♂), ♀ June 14-21; ♂ May 10-June 14, Erigeron.

Nomada americana Kirby (1837) p. 269, pl. 6, fig. 3.

Holonomada placida (Cresson) (2 ♀ 5♂), ♀ September 7-13; ♂ September 7, Solidago.

Nomada placida Cresson (1864).

Holonomada superba (Cresson) (1 ♀ 2 ♂), ♀ June 14; ♂ August 5-16.

Nomada superba Cresson (1864).

Holonomada vincta (Say) (1 ♀ 7 ♂), ♀ July 30; ♂ July 19-30, Helianthus.

Nomada vincta Say (1837) p. 401.

Nomada cressonii Robertson (1 ♀ May 10).

Nomada cressonii Robertson (1893) p. 275.

Nomada sayi Robertson (2 ♀ 2 ♂), ♀ June 27; ♂ 21-27.

Nomada sayi Robertson (1900a) p. 293.

Xanthidium Luteoloides (Robertson) (1 ♂ May 12), Salix.
Nomada luteoloides Robertson (1895b) p. 124.
PASITIDAE
Holcopasites illinoensis (Robertson) (1 ♀ July 29).
Phileremus illinoensis Robertson (1891b) p. 64.
STELIDIDAE
Chelynia foederalis (Smith) (1 ♂ June 14).
Stelis foederalis Smith (1854) p. 275.
ANDRENIDAE
Andrena arabis Robertson (1 ♀ April 19), Claytonia.
Andrena arabis Robertson (1897) p. 334.
Andrena carlini Cockerell (25 ♀ 19 ♂), ♀ April 14-May 14; ♂ April 4-26, Claytonia, Crataegus.
Andrena carlini Robertson (1902b) pp. 190 and 192.
Andrena corni Robertson (1 ♀ June 20), Cornus.
Andrena corni Robertson (1900) p. 50.
Andrena erythronii Robertson (11 ♀), April 19, Claytonia, Salix.
Andrena erythronii Robertson (1891b) p. 53.
Andrena hirticincta Provancher (19 ♀ 14 ♂), ♀ September 7-20; ♂ August 19-September 13, Solidago.
Andrena hirticincta Viereck (1916) pp. 710, 711, 715, 718.
Andrena nasonii Robertson (2 ♀ 1 ♂), ♀ April 19-May 3; ♂ April 13, Crataegus.
Andrena nasonii Robertson (1895b) p. 120.
Andrena nubecula Smith (7 ♀), September 2-20, Solidago.
Andrena nubecula Smith (1853) p. 117.
Andrena platyparia Robertson (19 ♀ 17 ♂), ♀ June 14-21; ♂ June 14-21, Cornus, Prunus.
Andrena platyparia Robertson (1895b) p. 119.
Andrena salictaria Robertson (2 ♀ 33 ♂), ♀ April 12; ♂ April 12-19, Salix.
Andrena salictaria Robertson (1905) p. 236.
Opandrena miserabilis (Cresson) (1 ♀ May 14), Claytonia.
Andrena flavo-clypeata Robertson (1891b) p. 55, also earlier references.
Opandrena cressonii (Robertson) (3 ♀ 10 ♂), ♀ May 14-June 21; ♂ May 14-19, Salix, Claytonia, Prunus.
Andrena cressonii Robertson (1891b) p. 56.
Opandrena ziziae (Robertson) (5 ♀), June 14.
Andrena ziziae Robertson (1891b) pp. 55, 56.
Opandrena serotina (Cresson) (20 ♀ 4 ♂), ♀ June 27-July 5; ♂ June 27-28, Rhus.
Andrena serotina Robertson (1893) p. 148.
Parandrena andrenoides (Cresson) (12 ♀ 4 ♂), ♀ April 12-May 4; ♂ May 4, Salix.
Panurgus andrenoides Cresson (1878a) p. 62.
Pterandrena aliciae (Robertson) (37 ♀ 22 ♂), ♀ July 30-August 19; ♂ July 30-August 16, Helianthus, Rudbeckia.
Andrena aliciae Robertson (1891b) p. 57.
Pterandrena helianthi (Robertson) (39 ♀ 32 ♂), ♀ August 5-September 20; ♂ July 27-September 12, Helianthus.
Andrena helianthi Robertson (1891b) p. 55.
Pterandrena krigiana (Robertson) (2 ♀), June 20, Krigia.
Andrena krigiana Robertson (1901) p. 229.
Pterandrena pulchella (Robertson) (2 ♀), August 30-September 5, Helianthus.
Andrena pulchella Robertson (1891b) p. 57.

Pterandrena rudbeckiae (Robertson) (6 ♀), June 27-July 11, Rudbeckia.
Andrena rudbeckiae Robertson (1891b) p. 56.
Pterandrena solidaginis (Robertson) (59 ♀ 19 ♂), ♀ September 7-13; ♂ September 2-13, Solidago.
Andrena solidaginis Robertson (1891b) p. 55.
Ptilandrena erigeniae (Robertson) (83 ♀ 44 ♂), ♀ April 6-May 3; ♂ April 6-May 3, Claytonia, Hepatica.
Andrena erigeniae Robertson (1891b) p. 52.
Ptilandrena g. maculati (Robertson) (4 ♀), May 14, *Geranium maculatum*.
Andrena g. maculati Robertson (1897) p. 333.
Ptilandrena polemonii (Robertson) (4 ♀ 3 ♂), ♀ May 3-10; ♂ May 3, Polemonium.
Andrena polemonii Robertson (1891b) p. 54.
Trachandrena claytoniae (Robertson) (1 ♀ 5 ♂), ♀ May 14; ♂ May 14, Claytonia.
Andrena claytoniae Robertson (1891b) p. 59.
Trachandrena forbesii (Robertson) (3 ♂), April 12, Salix.
Andrena forbesii Robertson (1891b) p. 59.
Trachandrena heraclei (Robertson) (1 ♀ April 4), Salix.
Andrena heraclei Robertson (1897) p. 336.
Trachandrena hippotes (Robertson) (3 ♀), May 14, Prunus.
Andrena hippotes Robertson (1895b) p. 120.
Trachandrena mariae (Robertson) (2 ♀ 9 ♂), ♀ April 12; ♂ April 12, Salix.
Andrena mariae Robertson (1891b) p. 58.
Trachandrena quintilis (Robertson) (1 ♀), June 6.
Andrena quintilis Robertson (1898) p. 46.

COLLETIDAE

Colletes americanus Cresson (2 ♀ 3 ♂), ♀ September 20-October 4; ♂ August 30-September 7, Aster, Solidago.
Colletes americana Cresson (1868).
Colletes armatus Patton (13 ♀), August 23-September 13, Aster, Solidago.
Colletes armata Patton (1879a) p. 365.
Colletes compactus Cresson (12 ♀ 18 ♂), ♀ September 12-October 4; ♂ August 30-September 12, Aster, Solidago.
Colletes compacta Cresson (1868) p. 166.
Colletes eulophi Robertson (63 ♀ 25 ♂), ♀ July 18-August 5; ♂ June 6-September 2, Allium.
Colletes eulophi Robertson (1891b) p. 61.
Colletes inaequalis Say (1 ♀), May 17.
Colletes inaequalis Say (1837) p. 391.
Colletes latitarsis Robertson (1 ♀), July 25.
Colletes latitarsis Robertson (1891b) p. 60.
Colletes nudus Robertson (1 ♀), July 11, Ceanothus.
Colletes nudus Robertson (1898) p. 43.
Colletes validus Cresson (24 ♀ 47 ♂), ♀ May 3-4; ♂ May 3-4, Salix and nests in sand of lake shore near Zion City.
Colletes valida Cresson (1868) p. 165.
Colletes willistonii Robertson (1 ♂ June 27).
Colletes willistonii Robertson (1891b) p. 60.

DUFOUREIDAE

Halictoides marginatus (Cresson) (6 ♀ 35 ♂), ♀ August 30-September 5; ♂ August 30-September 12, Helianthus.
Panurgus marginatus Cresson (1878a) p. 62.

HALICTIDAE (Females winter over, produce other females, then males, in most cases).

Agapostemon radiatus (Say) (9 ♀ 14 ♂), ♀ May 10-September 13; ♂ July 31-August 30, widespread and numerous.

Halictus radiatus Say (1837) p. 394.

Agapostemon splendens (LePéletier) (5 ♂), August 19, oak dunes.

Halictus splendens LePéletier (1836-46) p. 283.

Agapostemon texanus Cresson (4 ♀ 4 ♂), ♀ May 10-October 4; ♂ August 4-September 20, widespread, Cirsium and Composites for males.

Agapostemon texanus Cresson (1872) p. 255.

Agapostemon viridulus (Fabricius) [*virescens* (F.)] (117 ♀ 17 ♂), ♀ June 14-October 4; ♂ August 4-October 5, very widespread and numerous Pentstemon.

Apis viridula Fabricius (1775) p. 342.

Augochlora fervida Smith (1 ♀ August 5), oak dune.

Augochlora fervida Smith (1853) p. 81.

Augochlora viridula F. Smith (27 ♀), May 10-August 19, widespread and numerous.

Augochlora viridula Smith (1853) p. 81.

Chloralictus albipennis (Robertson) (36 ♀ several ♂), ♀ June 15-July 18, Melilotus.

Halictus albipennis Robertson (1890) p. 317.

Chloralictus coeruleus (Robertson) (16 ♀ several ♂), ♀ June 28-August 12, Monarda.

Halictus coeruleus Robertson (1893) p. 146.

Chloralictus cressonii (Robertson) (53 ♀ numerous ♂), ♀ May 10-August 14, general and numerous.

Halictus cressonii Robertson (1890) p. 317.

Chloralictus graenicheri Ellis (5 ♀), July 19, sandy soil.

Halictus graenicheri Sandhouse (1924) p. 4.

Chloralictus pilosus (Smith) (31 ♀ numerous ♂), ♀ May 3-July 19, very widespread and general.

Halictus pilosus Smith (1853) p. 71.

Chloralictus sparsus Robertson (27 ♀ several ♂), ♀ May 10-August 26, very widespread and numerous.

Chloralictus sparsus Robertson (1902) p. 249.

Chloralictus tegularis (Robertson) (15 ♀ several ♂), ♀ June 5-August 21, widespread and numerous.

Halictus tegularis Robertson (1890) p. 318.

Chloralictus versatus Robertson (97 ♀ numerous ♂), ♀ June 2-August 21, most widespread and very numerous.

Chloralictus versatus Robertson (1902) p. 249.

Chloralictus vierecki Crawford (17 ♀), July 19, sandy soil, Ceanothus.

Halictus vierecki Sandhouse (1924) p. 4.

Chloralictus zephyrus (Smith) (50 ♀ numerous ♂), ♀ July 4-18, widespread and numerous.

Halictus zephyrus Smith, F. (1853) p. 68.

Curtisapis coriacea (Smith) (99 ♀ 16 ♂), ♀ May 10-September 20; ♂ August 4-October 12, widespread and general.

Halictus coriaceus Smith, F. (1853) p. 70.

Curtisapis forbesii (Robertson) (22 ♀ 2 ♂), ♀ April 12-August 4; ♂ July 15-August 26, Salix, general.

Halictus forbesii Robertson (1890) p. 315.

Curtisapis fuscipennis (Smith) (2 ♀), June 21-August 2, Rhus.

Halictus fuscipennis Smith, F. (1853) p. 67.

Dialictus anomalus Robertson (36 ♀ some ♂), ♀ June 14-July 29, Pentstemon, Rudbeckia; visit records differ much from Robertson.
Halictus anomalus Robertson (1892).

Evylaeus arcuatus (Robertson) (81 ♀ 14 ♂), ♀ May 14-July 29; ♂ August 2-September 12, Rhus, widespread.
Halictus arcuatus Robertson (1893) p. 145.

Evylaeus foxii (Robertson) (1 ♀), August 4, Aster.
Halictus gracilis Robertson (1890) p. 316.

Evylaeus nelumbonis (Robertson) (4 ♀), June 28, *Nymphaea lutea*.
Halictus nelumbonis Robertson (1890) p. 316.

Evylaeus pectinatus (Robertson) (1 ♀), July 11.
Halictus pectinatus Robertson (1890) p. 315.

Evylaeus pectoralis (Smith, F.) (36 ♀ 1 ♂), ♀ May 10-August 7; ♂ July 30, widespread and numerous.
Halictus pectoralis Smith (1853) p. 68.

Evylaeus quadrimaculatus (Robertson) (88 ♀ 18 ♂), ♀ June 14-August 15; ♂ August 4-9, Sonchus, Rudbeckia.
Halictus quadrimaculatus Robertson (1890) p. 316.

Evylaeus truncatus (Robertson) (13 ♀) July 4-15, Ceanothus.
Halictus similis Robertson (1900) p. 52.

Halictus lerouxii LePéletier (21 ♀ 21 ♂), ♀ May 10-August 4; ♂ July 29-September 13, widespread and numerous.
Halictus lerouxii LePéletier (1836-46) p. 372.

Halictus parallelus Say (2 ♀), July 4, Rhus.
Halictus parallelus Say (1837) p. 397.

Halictus texanus (Cresson) (19 ♀), July 4-5, Sandy soil, to light at night, our only dusk flyer.
Sphecodes texana Cresson (1872) p. 249.

Odontalictus ligatus (Say) (243 ♀ 102 ♂), ♀ May 10-September 12; ♂ July 26-October 4, extremely widespread and numerous, favors Compositae.
Halictus ligatus Say (1837) p. 396.

Oxystoglossa confusa (Robertson) (64 ♀ 40 ♂), ♀ May 10-October 10; ♂ August 2-September 12, very widespread and numerous.
Augochlora confusa Robertson (1897) p. 324.

Oxystoglossa pura (Say) (2 ♀ 2 ♂), ♀ May 10-October 4; ♂ August 4-16.
Halictus purus Say (1837) p. 395.

Oxystoglossa similis (Robertson) (49 ♀ 4 ♂, or mixed with *O. confusa*), ♀ May 10-July 26; ♂ July 19-August 30, widespread.
Augochlora similis Robertson (1893) p. 146.

Paralictus cephalicus (Robertson) (2 ♀), July 26, one more pale than other, both much more than Robertson's. Cirsium, Cornus.
Halictus cephalicus Robertson (1892).

Seladonia fasciata (Nylander) (47 ♀ 7 ♂), ♀ May 10-October 4; ♂ July 26-September 5, widespread and numerous.
Halictus fasciatus Robertson (1895b) p. 117.

Machaeris stygia (Robertson) (1 ♀ 1 ♂), ♀ August 16; ♂ September 2.
Sphecodes stygius Robertson (1893) p. 145.

Proteraner ranunculi (Robertson) (1 ♀ 1 ♂), ♀ June 15; ♂ June 15, Apocynum.
Sphecodes ranunculi Robertson (1897) p. 318.

Sphecodes arvensis Patton (1 ♀), July 26, Pycnanthemum.
Sphecodes arvensis Patton (1880) p. 230.

Sphecodes clematidis Robertson (1 ♀), April 12.
Sphecodes clematidis Robertson (1897) p. 320.
Sphecodes heraclei Robertson (3 ♀), August 5-28, Solidago.
Sphecodes heraclei Robertson (1897) p. 318.
Sphecodes minor Robertson (1 ♀), July 4.
Sphecodes minor Robertson (1898) p. 45.
Sphecodium cressonii Robertson (1 ♀), June 28, above Halictid nests.
Sphecodium cressonii Robertson (1903) p. 104.
Sphecodium pimpinellae (Robertson) (1 ♀), May 10, Taenidia.
Sphecodes pimpinellae Robertson (1900) p. 51.
MACROPIDIDAE
Macropis ciliata Patton (3 ♀ 2 ♂), ♀ July 5-26; ♂ July 5, Steironema.
Macropis ciliata Patton (1880a) p. 31.
Macropis morsei Robertson (12 ♀, 1 ♂), ♀ July 5-26; ♂ July 5, Steironema.
Macropis morsei Robertson (1897) p. 336.
PANURGIDAE
Calliopsis andreniformis Smith (45 ♀ 20 ♂), ♀ June 16-August 19; ♂ June 28-August 19, prairie.
Calliopsis andreniformis Smith, F. (1853).
Heterosarus parvus (Robertson), (1 ♂), July 4, Ceanothus.
Calliopsis parvus Robertson (1892).
Pseudopanurgus albitarsis (Cresson) (7 ♀ 13 ♂), ♀ August 19; ♂ July 15-September 5, Helianthus.
Panurgus albitarsis Cresson (1872) p. 260.
Pseudopanurgus compositarum (Robertson) (1 ♀), October 10, Aster.
Calliopsis compositarum Robertson (1893) p. 274.
Pseudopanurgus labrosus (Robertson) (4 ♂), August 19-September 5, Rudbeckia.
Panurginus labrosus Robertson (1898) p. 48.
PROSOPIDIDAE
Prosopis illinoensis Robertson (51 ♀ 5 ♂), ♀ June 15-September 13; ♂ June 15-August 12, Solidago.
Prosopis illinoensis Robertson (1896a) p. 138.
Prosopis pygmaea Cresson (47 ♀ 12 ♂), ♀ June 14-September 7; ♂ June 14-August 4, widespread, Apocynum.
Prosopis pygmaea Cresson (1869) p. 272.
Prosopis saniculae Robertson (2 ♀), August 9-23, Daucus.
Prosopis saniculae Robertson (1896a) p. 137.
Prosopis sayi Robertson (17 ♀ 3 ♂), ♀ June 15-August 26; ♂ June 14-August 4, Apocynum.
Prosopis Sayi Robertson (1904) p. 273.
Prosopis ziziae Robertson (57 ♀ 15 ♂), ♀ June 15-August 19; ♂ June 13-August 12, Apocynum, Zizia, widespread.
Prosopis ziziae Robertson (1904) p. 273.

Data given in the above list, and more specific, fragmentary records not included, seemed to be insufficient for generalizations concerning suspected bee-adaptations. For this reason it was determined to compare the Carlinville and Chicago areas and, if sufficient similarity of fauna and flora was indicated, certain of Robertson's data could be tested to see if they would supply predictions of bee-adaptations for experimental confirmation or dis-

proof or for later confirmation or negation by additional collecting data from the Chicago region.

III. COMPARISON OF THE CARLINVILLE AND CHICAGO AREAS

A. FLORAS OF THE TWO REGIONS

Carlinville, Illinois, is located almost on a line between Chicago and St. Louis, and is approximately 250 miles southwest of Chicago, south of Springfield, almost in the Austro-riparian Area of the Austral Zone of Merriam (1898). Often shown in the prairie country, it is much more characteristically surrounded by mesophytic forest, running to what may be called the flood-plain type in the Chicago area. Sections of country having prairie characteristics are readily available but there is nothing in the region to compare with the dune series of the Chicago area.

Chicago, and its immediate vicinity, becomes the focus of several divergent lines of plant groups. Northern species work down the lake from Wisconsin, eastern species move in through Indiana with a very unique flora characteristic of the dunes, southern species move up and are available in the dunes, while the more characteristically western species of Iowa and beyond are also to be expected. Both Chicago and Carlinville, however, are included in Merriam's Carolinian Area of the Upper Austral Zone.

Fuller (1925) describes the more clearly defined plant communities (called by him "associations") of the Chicago region. These are given in Appendix B. In his paper, Fuller lists the more common plants of these communities and omits all weeds and ruderals.

Robertson, in numerous papers (1887, 1889, 1890a, 1891a, 1892a, b, 1893a, 1894a, 1895, 1896b, c, 1898a and 1899a) reported studies in the Carlinville area and in a work entitled "Flowers and Insects" (1928) presented a bibliography and gave a complete list of the flowers he had studied, together with the observed visitors and other data.

A comparison of the numbers of plant species found in the Carlinville region and in the Chicago region shows the expected similarities. Table I shows the highest percentage of plants in both regions to be found in high prairie, but the data on plants not listed in Fuller (1925) give a mesophytic character to the Carlinville area.

In addition to the plants considered in Table I, the majority of plants studied by Robertson (1928) and not given by Fuller (1925) yet stated by Fuller verbally or by Pepoon (1927) to be found in the Chicago area are plants primarily found in flood-plain, climax, red and white oak, or prairie communities. Numbers of these studied by Robertson are as follows: in flood-plain, 45 or 28.5%; in climax, 12 or 7.6%; in red and white oak, 20 or 12.6%; in low prairie, 27 or 17.0%; in high prairie, 10 or 6.3%; and in all

other communities, 44 or 27.8%. These figures do not include weeds, ruderals, introduced plants, and others not belonging to one or more of the endemic communities.

The figures in Table I and the additional ones of the preceding paragraph, tend to justify the assumption that there are decided similarities in the Chicago and Carlinville areas, and that bees found common to both areas might be expected to present, in the Chicago region, flower-reactions essentially similar to those exhibited and reported in the region of Carlinville.

TABLE I—*Comparison of numbers of flowers in the communities of Fuller with the numbers of these flowers studied by Robertson*

Community of Fuller	Flowers given in Fuller (1925)	Number of these flowers studied by Robertson (1928)	Percentage studied by Robertson
I–1	8	0	0.0
I–2	19	4	21.0
I–3	24	10	41.7
I–4	46	18	39.1
I–5	91	42	46.1
I–6	84	37	44.0
I–7	75	37	49.3
I–8	26	9	34.6
II–1	28	19	67.9
II–2	80	64	80.0
III	96	28	29.2
IV	69	7	10.1
V	13	5	38.5
VI	53	28	52.8
VII	129	77	59.8
VIII	47	17	36.2
Total	888	402	45.2

However, as stated, distinct differences in the flora are also to be noted, particularly a preponderance of more mesic plants in the Carlinville area, and these differences will also tend to make the results obtained from observations in the Chicago region differ from conclusions drawn in the Carlinville area. These differences become more apparent when the bees are considered.

B. BEE FAUNAS OF THE TWO REGIONS

The data to be presented on this point are based on the work of Robertson published both as separate papers and finally in his "Flowers and Insects" (1928). It was found necessary to rework these data from the form given by Robertson, in which the flowers were listed by families and genera, with bee visitors added. For use in the present work, the bees were arranged by

families and genera and the flowers Robertson found them on were tabulated after each bee species. Degree of abundance of visits to each flower was also carried over from Robertson's book.

When completed, this list was compared with the list given in the partial check-list (Section II) and it was observed that some bees reported from Chicago were absent from Carlinville, and a large number reported from Carlinville had not yet been taken in Chicago. Yet of the bees reported from Chicago for 1930 and 1931, 157 of the 169 or 92.9% are given by Robertson, though species now unidentified will doubtless cut down this percentage when identified. Of those given by Robertson, 157 of the 297 or 52.8% are reported from Chicago, and this percentage will doubtless be increased with further identification and collection.[3] These figures would seem to further justify extensive use of Robertson's data in studies made in this region.

C. The Flower-Bee Relations of the Two Regions

Although it has not been possible to obtain more than an indication of the flower-bee relations for the Chicago region, data have been obtained which would seem to show that, in certain cases at least, Robertson's Carlinville results can be approximately confirmed for the Chicago region.

The 27 species of flowers given in Table II have been observed closely and detailed lists of the bees visiting them in the Carlinville and Chicago regions have been made up. It is not practicable to publish either of these lists. In study of the summary of this comparison in Table II it must be remembered that "as yet unidentified" species will alter final results and it is to be inferred that further collecting from year to year in Carlinville would also, perhaps, shift Robertson's results, to a certain degree.

In Table II, following the assigned number and the name of the flower species of each of the 27 examples chosen, the next column gives the number of species of bees, common to both regions, found on the plant or flower species. For example, 18 of the bee species recorded by Robertson as visiting *Rhus glabra,* have also been taken on this species by the writer in the Chicago region. The next column gives 0 for *Rhus glabra* and indicates that no additional species not taken by Robertson on this flower have been taken in the Chicago area. Then the 18 of the next column indicates that Robertson recorded 18 additional species on this flower, which have not yet been taken by the writer on the same flower. The final column compares the percentage of species common to both regions with the total number of bee species recorded from both regions as visiting the flowers of *Rhus glabra.*

Attention is called to the fact that these data are not submitted as evidence for adaptation of bees to certain plant species. These data are believed to

[3] In an earlier footnote, in connection with the check-list, 19 species were listed as identified or collected in 1932. Of these 19, 16 appear in Robertson 1928, thus raising the number of Carlinville bees found in the Chicago Region to 173 out of 297 or 58.2%.

furnish evidence that, of a given number of bee species taken during many years of collecting on a flower in the Carlinville region, a large percentage of the same restricted list of bees, and relatively few others, will be taken on the same flower in the Chicago region. Naturally the more "general" bees (visiting a considerable variety of flowers) will appear several times in any list and will be collected where a rare bee will be missed. However, a long list of bee species will appear in even as short a list of flowers as that of Table II.

TABLE II—*Comparisons of the species of bees that visited twenty-seven selected flower examples found in both the Carlinville and Chicago regions*

Plant Species	Species of bees common to both regions	Species taken only in Chicago	Species taken only in Carlinville	Percentage of species taken in both regions
Rhus glabra	18	0	18	50.0
Apocynum androsaemifolium	4	4	2	40.0
Asclepias syriaca	7	0	19	26.9
Impatiens biflora	6	1	2	66.6
Campanula americana	10	1	6	58.8
Sambucus canadensis	6	1	2	66.6
Cirsium lanceolatum	16	2	15	48.4
Rudbeckia hirta	18	4	9	58.0
Silphium integrifolium	13	0	8	61.9
Vernonia fasciculata	16	5	10	51.6
Geranium maculatum	13	0	22	37.1
Monarda fistulosa	14	2	14	46.6
Baptisia leucantha	1	1	0	50.0
Melilotus alba (intr.)	24	0	20	54.5
Sanguinaria canadensis	4	0	3	57.1
Phlox glaberrima	0	0	0	100.0
Claytonia virginica	33	0	25	56.9
Steironema ciliatum	1	3	1	20.0
Hepatica acutiloba	5	1	6	41.8
Ceanothus americanus	16	3	8	59.2
Prunus serotina	10	1	20	32.2
Rosa humilis	8	0	6	57.1
Rubus villosus	14	0	36	28.0
Cephalanthus occidentalis	7	0	24	22.5
Philadelphus grandiflorus	4	1	6	36.3
Gerardia grandiflora	5	1	4	50.0
Pentstemon laevigatus	19	6	3	67.8
Total	292	37	289	47.2
Species involved	85	29	121	

The bee-species flower records common to both regions on the 27 flowers total 292. These are made up from records of 85 different species of bees. The bee species records from these 27 flowers, given by Robertson in addition to the 292 common to both regions, total 289. These records are made up by 121 species of bees, 55 of which have not yet been taken at all by the writer, while 66 of them have been taken by him but not in the relations to flower species indicated by Robertson in this column. Then, finally, 37 species records are given for the 27 flowers, obtained in the Chicago region and based on 29 species of bees all collected by Robertson but not in the flower

relations given by this column. It will also be observed that if 292 flower bee-species records are common to both regions for these 27 flowers, and if 618 total flower bee-species records are included, 47.2% of the records will be shown as being similar in both the regions under discussion.

Data of the collection made in the Chicago region confirm in general the relations laid down by Robertson (1928). *Evylaeus nelumbonis* was taken only on the flowers of *Nymphaea advena* and, as Robertson indicates, no other visitor was observed. Species of *Salix* presented the wide variety of spring Andrenidae suggested by Robertson. Helianthus and its allies showed the great numbers of visits of *Melissodes obliqua, M. coloradensis,* and *M. agilis,* of *Pterandrena helianthi,* and of the unique *Halictoides marginatus;* Solidaginis presented its oligolege *Pterandrena solidaginis,* and its large numbers of *Colletes armatus* and *C. compactus;* Cirsium yielded many specimens of *Melissodes cnici, Triepeolus donatus,* and *Bremidae;* and Rudbeckia led in *Tetralonia dilecta, Melissodes trinodis,* and *Pterandrena aliciae.*

Certain variations would be expected in the Chicago region, from relations prevailing in the Carlinville region. One striking confirmation yet variation is indicated by relations of Steironema and Macropis. Robertson (1926) includes *Macropis steironematis* as an oligolege of Steironema. None of this species were taken in the Chicago area, but two species of Macropis not reported from Carlinville were taken on plants of this genus. These bees were *Macropis ciliata* and *M. morsei.*

The Chicago region yields the conspicuous *Andrena hirticincta* which does not occur near Carlinville. Here is found the northern *Chloralictus graenicheri* and the eastern *C. viereckі,* neither of which go much further south. The striking *Halictus texanus* occurs in Wisconsin, the Dakotas, Texas, and in the Southern Chicago region, but is not found near Carlinville. The northern Bremidae come into the northern limits of the Chicago area and are of course absent from Carlinville. Not only does the interesting *Zaodontomerus calcaratus* occur in this region, but the eastern *Zaodontomerus metallicus* has been taken in the dunes region and thus is presented the phenomenon of three species, these two and *Ceratina dupla,* all found in one region and all with the females indistinguishable. The more northern *Colletes valida* was very numerous along the western shores of Lake Michigan.

The data given in this section indicate that it is justifiable to expect a majority of the bees occurring in both areas to bear in this region the same relations to plants that they bear to the same species of plants in the Carlinville area.

IV. COMPARISON OF AVAILABLE DATA CONCERNING THE APPARENT ADAPTATIONS OF CERTAIN BEE SPECIES TO PLANT COMMUNITIES, WITH DATA CONCERNING BEE SURVIVAL

In this section it is proposed to examine available observational data in an attempt to ascertain whether biotic factors or physical factors are of primary importance in determining what habitats shall be frequented by a given species of bee. If it is decided that a sufficient number of species are apparently governed to a large extent by physical factors in their distribution among and visits to various habitats, then experimental studies on certain of these species or larger groups, under controlled conditions of temperature and humidity, should offer some corroboration of apparent adaptation to these particular habitats, for the habitats themselves are to a large extent products of temperature and humidity.

All of Robertson's (1928) observations on the visits of bees to flowers, which relate to plants that are known to occur in the Chicago area, were transferred over into a detailed list to give a prediction of the number of flower-species that each of his bees would be expected to visit in the Chicago area, with information concerning the number of species of flowers visited either frequently or abundantly in each plant community. To supplement these records, others were available from the 1930 and 1931 collections made in this area.[4]

These data are drawn upon later in this work, to furnish comparison records for certain species, genera, and families of bees, in order to determine if any correlation exists between the character of the physical conditions of the communities most characteristically visited by the bees, and the type of physical conditions maintained experimentally in the laboratory, under which the given group of bees survives for the maximum period of time.

RELATIONS OF BEES TO PARTICULAR PLANT COMMUNITIES

1. Species that seem Definitely to be Expected in Certain Communities Only, according to Robertson's Data, with Confirmation from Local Data Where Possible.

Among the *Anthophoridae*, *Emphoropsis floridana* is interesting as being placed in only I-7 and VII (see Appendix B for plant community symbols). However, only males are recorded and they have not been taken by the writer. Clisodon may be called "mesic." Others of the family are quite generally distributed.

Apis mellifera has become a very cosmopolitan bee following its intro-

[4] The writer wishes here to acknowledge the assistance of Dr. Charles H. Seevers, Mr. E. Morton Miller, and Dr. B. H. Willier, in the collection of specimens, and the assistance of Mrs. Hazel M. Pearson in the checking of records and manuscript, and the collecting of specimens and preparing of labels and records.

duction by man, that great disturber of ecological factors. This introduced species appears to exert an influence upon native bees, which is visible to any student of the native species. So efficient is it as a collector of pollen and honey and so ubiquitous has it become, there can be no question but what its inroads cause a serious diminution in the food supply of native bees, particularly in bad seasons.

In the *Bombidae (Bremidae)* listed by Robertson (1928), *Bombias scutellaris* is distinctly a prairie bee, most abundant in community II-2. *Bombus americanorum* is the most cosmopolitan of the *Bombidae* and of the bees as a whole, exceeding even *Apis mellifera*. Not only has it been recorded to make 346 flower-community visits, but very many of these are frequent or abundant. *Bombus consimilis* would seem to react most favorably to I-6, 7, and VII, adapted more to moist woods than to drier conditions. On the other hand, the inquilines *Psithyrus laboriosus* and *P. variabilis* seem to fall into open country of prairie, with a rather striking absence or near absence from the series of dune or morainic uplands.

Ceratina dupla is another very widely distributed bee present in abundance upon numerous flowers in many communities.

Emphor bombiformis is absent, apparently, from the dune-morainic series and has not yet been taken by the writer. The same holds true for *Melitoma taurea*.

Epeolus bifasciatus, Triepeolus concavus, T. concolor, T. lunatus, and *T. remigatus* are the most striking examples of the general trend of adaptation of this family to prairie, particularly high prairie.

Among the *Euceridae* it is of interest to note that Melissodes is predominantly a prairie bee, while Tetralonia runs to moister woods of the dune or morainic series and to other associations such as flood-plain, with comparative absence from prairie.

Considering the *Megachilidae,* we observe that Centrosmia, Ceratosmia, Diceratosmia, and *Osmia pumila* run to I-6, 7, and VII; that Gnathosmia might seem to run to II-2; and that others of Osmia are more general. *Hoplitis cylindricus* would seem to favor I-4, II-2, and VI, regions with less humidity; while *Neotrypetes productus* runs mainly to II-2. *Megachile addenda* is found mainly in I-5 and I-6; *M. brevis* is very cosmopolitan with 147 flower-community visits but is dominantly in prairie. *M. petulans* is general but very well represented in III-5; *M. strophostylis* is to be expected only in the dry I-2 and I-3; and *Sayapis pugnata* and *S. sayi* are dominantly II-2. The common Xanthosarus is also very dominantly prairie though rather well distributed through the communities. Most visits and abundant visits of Coelioxys are recorded from II-2.

In the family *Nomadidae* there is a rather general distribution of certain species, with others showing definite restrictions. Numerous visits to communities III and IV, particularly III-3, are to be noted.

Holcopasites illinoensis runs to I-4 and II-2 both of which are regions of higher evaporation rate.

Microstelis lateralis and *Stelidium trypetinum* of the Stelididae both run most commonly to II-2.

Most bees of the genus Andrena are to be expected in I-5, 6, 7, and VII. There are some with records in I-3 and 4, as well as a considerable number in III and VI. This genus is practically absent from II. *Opandrena cressonii, O. miserabilis,* and *O. personata* are numerous and cosmopolitan. The first of these is very characteristically a flood-plain bee, though it shows frequent records in I-3 and I-4. All three show a greater proportionate abundance in VI than is observed among the bees considered above. *O. personata* is most characteristically found in I-6 of the dune or morainic series. Among the *Pterandrena,* only *P. krigiana* with its records in I-5 and 6 and *P. lauracea* with no records save I-5 and 6 deviate from the general rule of predominance in prairie. *P. rudbeckiae* shows an abundant record also in both I-8 and VIII. The three *Ptilandrena* species show no visits whatsoever save to I-6, 7, and VII, where all are found. In Trachandrena, III-3 figures abundantly. Several of these bees run to a rather general distribution, with emphasis on I-5, 6, 7, and VII. However, *T. forbesii, T. hippotes,* and *T. mariae* favor I-3, 4, and 5 in the dune or morainic series, while *T. heraclei, T. obscura,* and *T. quintilis* are practically absent from the series. The two latter show only records in II-2 of prairie. *Trachandrena spiraeana* shows an abundant record only in V.

In the *Colletidae,* there is also a variety of distribution. *Colletes albescens* is recorded from I-4 and II-2; *C. aestivalis, C. americanus, C. productus, C. robertsonii, C. similis,* and *C. speciosus* favor II-2 of prairie; *C. brevicornis* falls only into VI; *C. latitarsis* runs to I-3, and I-5; while the others are more general in distribution.

Among the *Halictidae Agapostemon radiatus* and *A. splendens* may be considered as running more toward I-6, 7, and VII, though they hold up well in I-4 and prairie. *A. texanus* and *A. viridulus* run to prairie and more to I-4. Climax, I-7, is not much frequented by either. *Augochlora fervida* is very well represented in I-4, II-1, 2, and III-5. But *A. viridula* is dominantly in I-6, 7, and VII, though it also makes many visits to prairie. *Chloralictus albipennis* and *C. pruinosus* are most abundant in II-2, with good representation in I-2, 3, and 4. *C. coeruleus* favors VII, while *C. cressonii, C. sparsus,* and *C. zephyrus* are relatively more abundant in the more moist dune groups and in flood-plain. Other species of the genus are rather evenly distributed. *C. versatus* with 306 records is the most cosmopolitan of the species. *Curtisapis forbesii* seems to be best adapted, of the three in this genus, to dry conditions; while *C. coriacea* should be sought in red and white oak, in climax, and in flood-plain. Considering the genus *Evylaeus, E. arcu-*

atus centers in I-5 of the dune series, while *E. foxii* centers in I-4 according to frequency of visit, though more flowers of 1-7 are visited. *E. nelumbonis* is most characteristic of III-2, as the name might imply. *E. pectoralis* centers in II-2 and VII, while *E. quadrimaculatus* is most characteristic of VII. *Halictus lerouxii* is generally distributed, but *H. parallelus* centers in II-2 and I-4. *Odontalictus ligatus* is well distributed but predominantly visits both II-2 and II-1. It is really a prairie bee but a remarkable number of its visits are to Compositae. *Oxystoglossa confusa* is general and numerous; *O. pura* favors I-6, 7, and VII; and *O. similis* emphasizes I-4, II-2, and VI, though I-5, 6, and VII are often visited. *Seladonia fasciata* is rather evenly and generally distributed.

Considering the inquilines related to the genus Sphecodes, we find rather general distribution where sufficient data are available, though *Machaeris stygia, Sphecodes arvensis,* and *Sphecodium cressonii* are more probably to be found in II-2 than elsewhere.

Among the *Macropididae, Macropis steironematis* is the only one studied by Robertson. His data (1928) place this bee mainly in II-1. It is also to be sought in VIII and II-2.

Paranomia nortonii is to be expected in II-2. One other unidentified species of Nomiidae has been taken in II-2.

The Panurgidae are most characteristically found in prairie, though some are well distributed. *Pseudopanurgus labrosiformis* runs rather more toward VII than any of the other communities.

Prosopididae are generally distributed save *P. thaspii* and *P. saniculae* of VII only; *P. nelumbonis* of III-2; and *P. ziziae,* which is most characteristically to be found in II-2.

2. Percentage of Bees that can be Considered Restricted to Certain Communities.

Making use of the unpublished predictions concerning bee visits to plant communities (arrived at by applying Robertson's 1928 summary to Fuller's plant communities, Appendix B) it becomes evident that certain species may be said to offer indications of specializations that would fit them to specific environments; other are not so specialized. In comparing these two bee groups, only bees that have been taken on five or more species of flowers are included, unless they are oligoleges of one or more species of flowers. Out of 240 species given by Robertson (1928) with suitable information available, 168 or 70.0% may be said to show a broad distribution through plant communities of quite different physical characters. Seventy-two or 30.0% may be considered as visiting frequently or abundantly only one type of community or at least communities having somewhat similar conditions of humidity and evaporation.

3. Conclusions to be Drawn from Oligoleges.

The list of oligoleges given by Robertson (1926) is presented in Appendix A. Bee names followed by a "c" have been taken by the writer in the Chicago region. Bees followed also by a second "c" indicate species which have been observed collecting pollen from plants indicated by Robertson, and from no others. It will be observed that Robertson gives 83 species of oligoleges which are considered valid species in his 1928 book. Thirty-seven or 44.5% have been taken in the Chicago area, and 19 or 22.9% have been checked while collecting in this area and have not been disproved as oligoleges.

Comparison of the oligolege-species with the species apparently characteristic of one type of community shows that 29 or 36.6% of Robertson's 79 available oligoleges would be considered as fitting into one particular community with more emphasis than into others of different physical characteristics.

The question of oligoleges brings up Robertson's views concerning the interactions between flowers and bees. The present work has been questioning the possible existence of limited and selected bee constituents for many or certain of the plant communities of the Chicago area. Throughout all of the numerous papers published by Robertson, there is no mention of plant communities. Robertson has, however, presented detailed studies of the structures and colors of flowers visited by various species of bees (1923 and 1925). It is thus evident that he considers the relations between flower and bee as paramount, with the bee, if necessary, following flowers of a given species or genus into regions of varying humidity and evaporation rate.

The following eight oligoleges, chosen from Robertson's list (1926) indicate the variable nature of the plant-community bee-visit predictions which can be made from Robertson's data (1928). Plant community symbols are explained in Appendix B. The name of the bee is followed by the name of the plant group to which the host belongs. This name in turn is followed by the number of plant species of the group which are visited for pollen by the oligolege (according to Robertson). The communities in which these host plants grow are then given.

Andrena arabis—Cruciferae—10 species. Taken by Robertson on three species, communities V, VII, 41, and 45. Species on which it was not taken occur in I-5, 6, 7, III-3, 21, 23, 32, 33, 34, and 41.

Andrena erythrogastra—Salix—5 species. Taken by Robertson on all five species, a true oligolege.

Andrena salictaria—Salix—5 species. Taken by Robertson on four species, communities I-3, 4, III-3, and VII. Salix occurs also in I-5 but this bee was not taken on the species that may occur in this community.

Iomelissa violae—Viola—6 species. Taken by Robertson on three species, communities I-5, 6, 7, II-2, and VII. Only one other community is represented by the three species not visited, namely, II-1.

Colletes latitarsis—Physalis—3 species. Taken by Robertson on all three species, communities I-3, 5, II-1, and 41.

Megachile generosa—Leguminosae—39 species. Taken by Robertson on five species, collecting pollen on three. Communities represented are I-2 and I-3, 27, 33, 34, 43, and 47. These and all other flower records seem to indicate a reaction that may be called positive to a sandy or dry environment. Other species in the family cover almost all communities and categories.

Melissodes cnici—Cirsium—4 species. Taken by Robertson on three of the four, the fourth blooming before the bee flies; communities II-1, II-2, and 29.

Emphor bombiformis—Hibiscus—3 species. Taken by Robertson on two of them, in communities VII and 47. The one not visited would come under the category 35.

4. Bee Species and Plant Communities.

Judging from the collection from the Chicago area, and from the predictions to be made from Robertson's collection (1928), it would seem to be clearly evident that a majority of the bee species will visit flowers in a number of different plant communities. In some cases, these visits will clearly

TABLE III—*Total species of bees from Robertson's data predicted by families as visitors to the various plant communities of Fuller*

Bee Families	Genera	Species	Communities																					
			I							II		III					IV				V	VI	VII	VIII
			2	3	4	5	6	7	8	1	2	1	2	3	4	5	1	2	3	4				
Long-tongued bees:																								
1. Anthophoridae	5	5	1	2	4	3	4	3	0	3	2	1	0	0	0	1	1	0	1	1	0	2	4	2
2. Apidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
3. Bombidae	3	10	6	5	6	8	8	7	4	8	9	3	4	7	0	8	6	3	5	6	4	9	8	7
4. Ceratinidae	2	2	0	2	2	2	2	2	1	1	2	1	1	2	0	1	1	0	2	1	2	2	2	2
5. Emphoridae	2	2	0	0	0	0	0	0	0	2	1	0	0	1	0	2	0	0	0	0	0	1	2	0
6. Epeolidae	3	18	2	2	6	12	8	1	7	13	16	2	0	3	0	13	11	0	0	0	0	11	11	12
7. Euceridae	9	32	13	11	15	22	15	8	8	21	27	5	0	9	0	16	11	2	1	1	1	19	24	17
8. Megachilidae	21	42	9	11	27	29	31	18	12	28	33	10	0	7	0	14	8	0	9	9	4	32	28	19
9. Melectidae	2	2	0	0	2	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0
10. Nomadidae	8	23	0	10	13	14	16	13	1	6	17	1	0	13	0	3	3	0	4	5	3	14	20	7
11. Pasitidae	1	2	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0
12. Stelididae	5	6	0	0	2	2	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0	3	1	2
13. Xylocopidae	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1
Total	63	146	32	44	80	94	84	54	54	84	115	24	6	43	0	60	43	6	23	24	15	96	103	70
Short-tongued bees:																								
51. Andrenidae	7	52	0	19	22	33	36	32	3	17	27	0	0	25	0	13	13	0	9	19	11	33	43	25
52. Colletidae	1	15	4	8	5	9	7	4	2	7	14	0	0	5	0	5	3	0	2	2	0	8	8	7
53. Dufoureidae	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1
54. Halictidae	17	56	9	28	39	43	41	34	19	27	45	10	12	38	0	29	20	5	17	23	12	42	48	33
55. Macropididae	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
56. Nomiidae	1	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
57. Panurgidae	8	16	0	0	3	9	4	2	5	11	12	1	0	0	0	9	8	0	0	0	0	4	11	7
58. Prosopididae	1	9	0	3	3	4	7	4	0	5	6	0	2	4	0	5	2	0	1	1	5	6	8	5
Total	37	151	14	58	73	101	95	76	29	69	107	11	14	72	0	62	47	5	29	45	28	93	120	80
Total All Bees	100	297	46	102	153	195	179	130	63	153	222	35	20	115	0	122	90	11	52	69	43	189	223	150

be made in search of food from any or from certain definite kinds of flowers. However, in other cases, these different plant communities will be seen to have certain definite physical characteristics that are much in common.

In the case where a species of bee visits several different plant communities, it is often still possible to add this bee species with confidence to the lists of animals found in these communities, provided that care is taken to record the time of year as well. It will then be possible to return to that community the next year and to expect, at the proper time, to collect that particular species of bee.

It seems reasonable to predict that as many or more bees will be found distinctive for each community as there are at present other insects, keeping in mind of course the total number of existing species, both of insects in general and of bees in particular. It is scarcely probable that the predictions based on Robertson's records alone, will be found seriously at variance with actual facts when more extensive collecting is done in this region.

TABLE IV—*Abundant and frequent records of bee visitors, predicted from Robertson's data by families for the various plant communities of Fuller*

Bee families	Communities																				
	I							II		III					IV				V	VI	VII	VIII
	2	3	4	5	6	7	8	1	2	1	2	3	4	5	1	2	3	4				
Long-tongued bees:																						
1. Anthophoridae	0	0	2	2	2	1	0	2	1	1	0	0	0	0	0	0	0	0	0	2	2	1
2. Apidae	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
3. Bombidae	1	1	5	4	6	6	1	6	6	1	0	4	0	5	3	1	1	1	1	4	6	3
4. Ceratinidae	0	1	1	1	2	0	1	1	2	1	0	2	0	1	1	2	1	1	0	2	2	1
5. Emphoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
6. Epeolidae	0	0	2	4	1	0	0	3	12	0	0	1	0	4	2	0	0	0	0	6	7	5
7. Euceridae	3	2	7	9	5	4	1	12	18	2	0	2	0	6	4	1	0	0	0	10	17	9
8. Megachilidae	4	4	8	9	15	6	2	11	18	2	0	3	0	3	1	0	1	1	0	18	14	5
9. Melectidae	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
10. Nomadidae	0	6	8	7	10	0	0	1	8	0	0	9	0	1	1	0	2	2	0	5	12	1
11. Pasitidae	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
12. Stelididae	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
13. Xylocopidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	9	15	36	38	43	18	6	37	69	8	1	22	0	21	13	3	6	6	2	48	63	27
Short-tongued bees:																						
51. Andrenidae	0	12	14	21	20	16	1	2	15	0	0	15	0	3	4	0	0	8	2	21	31	14
52. Colletidae	0	3	1	7	3	2	1	3	6	0	0	3	0	3	1	0	0	1	0	8	3	3
53. Dufoureidae	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
54. Halictidae	0	7	17	17	16	13	2	12	25	2	8	16	0	9	2	0	2	6	2	20	28	12
55. Macropididae	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
56. Nomiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
57. Panurgidae	0	0	2	4	3	0	2	7	9	1	0	0	0	3	2	0	0	0	0	2	7	5
58. Prosopididae	0	1	1	1	2	0	0	2	4	0	0	1	0	0	0	0	0	0	3	4	5	0
Total	0	23	35	52	44	31	6	27	62	3	8	35	0	18	9	0	2	15	7	53	74	36
Total All Bees	9	38	71	90	86	49	12	64	131	11	9	57	0	39	22	3	8	21	9	103	137	63

At this point it might be well to call attention to the fact that bees of the families *Apidae, Bremidae (Bombidae),* and *Halictidae* seem to be mostly general in distribution throughout the year as well as throughout various habitats, extremes of environment of course excepted. The other bees generally appear to be more restricted both in time and variety of communities visited.

TABLE V—*Total bee-species-flower-species visits predicted from Robertson's data by families for the various plant communities of Fuller*

Bee families	Communities																					
	I							II		III					IV				V	VI	VII	VIII
	2	3	4	5	6	7	8	1	2	1	2	3	4	5	1	2	3	4				
Long-tongued bees:																						
1. Anthophoridae	1	2	5	11	22	7	0	5	6	1	0	0	0	1	1	0	1	1	0	4	20	4
2. Apidae	4	5	10	21	25	29	5	19	39	1	1	7	0	15	4	1	1	4	3	19	61	11
3. Bombidae	10	10	27	73	130	75	12	88	174	3	4	17	0	55	22	3	5	9	7	63	214	29
4. Ceratinidae	0	2	8	21	38	30	5	14	40	1	1	8	0	9	5	0	3	2	0	29	60	9
5. Emphoridae	0	0	0	0	0	0	0	5	3	0	0	1	0	3	0	0	0	0	0	1	4	0
6. Epeolidae	2	2	7	19	7	1	7	39	75	2	0	3	0	25	12	0	0	0	0	19	33	16
7. Euceridae	15	13	25	46	51	25	16	81	149	5	0	11	0	49	18	2	1	1	1	37	111	25
8. Megachilidae	15	16	43	73	109	53	20	88	204	10	0	14	0	41	16	0	9	9	5	72	147	38
9. Melectidae	0	0	2	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0
10. Nomadidae	0	13	22	31	55	20	1	9	54	1	0	29	0	3	3	0	4	5	4	39	107	12
11. Pasitidae	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0
12. Stelididae	0	0	2	3	3	1	0	1	10	0	0	0	0	0	0	0	0	0	0	4	2	2
13. Xylocopidae	0	0	1	0	0	0	0	0	3	0	0	0	0	1	1	0	0	0	0	1	1	1
Total	47	63	153	299	440	241	66	349	763	24	6	90	0	202	82	6	24	31	26	289	761	147
Short-tongued bees:																						
51. Andrenidae	0	31	46	91	109	99	3	23	58	0	0	55	0	16	14	0	9	24	12	110	278	37
2. Colletidae	4	12	7	24	11	11	2	4	36	0	0	10	0	18	4	0	2	3	0	22	35	12
53. Dufoureidae	0	0	0	1	0	0	0	1	2	0	0	0	0	1	1	0	0	0	0	0	1	1
54. Halictidae	9	50	127	223	266	224	43	176	427	11	18	116	0	114	40	6	20	35	23	254	527	108
55. Macropididae	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	2
56. Nomiidae	1	0	2	1	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	1
57. Panurgidae	0	0	4	12	9	2	5	27	34	1	0	0	0	16	10	0	0	0	0	8	27	10
58. Prosopididae	0	3	5	16	19	14	0	15	38	0	3	8	0	16	2	0	1	1	6	22	68	9
Total	14	96	191	369	414	350	53	265	601	12	21	193	0	181	71	6	32	63	41	416	937	190
Total All Bees	61	159	344	668	854	591	119	615	1364	36	27	283	0	383	153	12	56	94	67	705	1698	337

B. ABUNDANCE OF BEES IN VARIOUS PLANT COMMUNITIES

As stated previously, the number and abundance of flower and community visits have been predicted for all of Robertson's flowers and their bee visitors, where both are known to occur in the Chicago region. If these records are summarized they afford information for comparison with data already presented by other workers, such as Park (1930) with Coleoptera. Although the community-bee relationships are not records but are calculated or predicted, and although they are drawn from the Carlinville area, which has no

dunes, there is sufficient similarity of plant species and bee species (Sections III A and B) to permit prediction in part for the dunes series of the Chicago region and to set forth certain conditions and relations which may be confirmed or disproved by future collecting.

In presenting this information concerning bee families and plant communities, four tables are given. The first one, Table III, gives the total numbers of species of bees in each family predicted for each plant community. Thus, Family 1, Anthophoridae, 5 genera, 5 species,—1 species visits community I-2, 2 visit I-3, 4 visit I-4, etc. Table IV predicts, from records of frequent or abundant visits only, the total number of species of bees of each family which will be found frequently or abundantly in the various communities. Table V gives total bee-species flower-species visits for each family of bees, predicted for each plant community. For example, if in a given family six species of bees are found in a given community, and six flowers are recorded for this community, in this table the records might show that each of the six bees visited each of the six flowers and thus the flower-species bee-species visits would be 36. A given species of bee thus may appear a

TABLE VI—*Summary of data of Tables III, IV, and V**

Community	No. of bee species predicted	No. of bee species abundant or frequent	No. of flower species visited	Ratio of flowers to bees	No. of flower bee-species visits
I-1	0	0	0	.....	0
I-2	46	9	4	1-11.5	61
I-3	102	38	10	1-10.2	159
I-4	153	71	18	1- 8.5	344
I-5	195	90	47	1- 4.15	668
I-6	179	86	56	1- 3.19	854
I-7	130	49	47	1- 2.76	591
I-8	63	12	12	1- 5.25	119
II-1	153	64	44	1- 3.47	615
II-2	222	131	73	1- 3.04	1364
III-1	35	11	2	1-17.5	36
III-2	20	9	3	1- 6.66	27
III-3	115	57	13	1- 8.84	283
III-4	0	0	0	.....	0
III-5	122	39	25	1- 4.88	383
IV-1	90	22	10	1- 9.0	153
IV-2	11	3	3	1- 3.66	12
IV-3	52	8	3	1-17.3	56
IV-4	69	21	4	1-17.25	94
V	43	9	5	1- 8.6	67
VI	189	103	34	1- 5.56	705
VII	223	137	120	1- 1.85	1698
VIII	150	63	18	1- 8.31	337
Total	2362	1032	551	1- 4.28	8616

*These record the numbers of bee species predicted for each plant-community, based on Robertson's 1928 data, the numbers of bee species predicted from the same source as visiting each plant-community abundantly or frequently, and the numbers of bee-species flower-species visits for each community, predicted also from Robertson's data. In addition to these comparisons, the ratios between bee species predicted and flower species from Robertson's 1928 work, known to be present, are also calculated, together with the numbers of these flower species in each community.

number of times in each community. This was of course not true in either Table III or Table IV. In Table VI, the total visits from all three preceding tables are given for comparison with the numbers of flower species in each community. A ratio between total species of bees and total species of flowers is also given for comparison.

Considering mainly the dune and morainic series, the prairie series, and the flood-plain plant community, more species of flowers are recorded from the red and white oak than from any other of the dune or "I" series. But these visits are exceeded in number by the numbers in the high prairie community and more than doubled by those in the flood-plain community. If the number of different species of bees found in the communities be considered, the peak falls at black oak or I-5. If only the frequent or abundant visits are considered, the peak falls in black oak or I-5, due to the visits of the short-tongued bees, principally Colletes and the *Panurgidae*. The peak of the long-tongued bees is in I-6. In the high prairie, there are 222 species of bees, 131 visiting abundantly or frequently the 73 species of flowers. Astonishingly enough, 223 species of bees, 137 abundantly or frequently, visit the 120 species of flowers of flood-plain. In other words, the same number of bees visit nearly twice the number of flower species. Table VI gives a ratio for each community between flower species found in, and bee species visiting, each community. The ratio for high prairie is seen to be 1 to 3.04. That of flood-plain is seen to be 1 to 1.85. In brief comment on this table, it might be said that the more species of plants in a given community, the fewer species of bees will visit each plant, which is what one would expect.

For the dune series, considering the families that have most species, while studying the abundant-frequent records only (Table IV), it may be noted that the peak for *Bombidae* falls in red and white oak, and climax; the peak of *Epeolidae* in I-5, or black oak; that of *Eucerida*e in black oak; that of *Megachilidae* strikingly in red and white oak; that of *Nomadidae* in red and white and with none at all in climax; the *Andrenidae* almost divided between black oak and red and white oak; *Colletidae* in black oak; and the *Halictidae* equally divided between pineland and black oak, with red and white oak a close third. The peak of *Panurgidae* falls in black oak, and that of *Prosopididae* in red and white oak. It is to be noted that there is then a complete absence of abundant or frequent records of the inquilines *Epeolidae* and *Nomadidae*, and of the short-tongued *Panurgidae*, from climax.

Halictidae and *Andrenidae* show the following comparative relationships: if the number of species of bees taken abundantly or frequently in high prairie and flood-plain be compared, there are 15 *Andrenidae* and 25 *Halictidae* in high prairie, and 31 *Andrenidae* and 28 *Halictidae* in flood-plain. But if the number of bee-flower-species records of these two families be compared for high prairie and flood-plain, we observe that there are 58 for *Andrenidae*

in high prairie, and 427 for *Halictidae*, but that for flood-plain there are 278 of *Andrenidae* and 527 of *Halictidae*. The differences observed may be explained by the fact that the prairie *Andrenidae* are practically all oligoleges of restricted plant groups.

C. Toleration Experiments to Test Physiological Adaptation of Bees to Physical Conditions of Plant Communities

1. Materials, Technique, and Apparatus Used.

a. Previous work with native bees.—Wild bees have scarcely been considered a favorite material for laboratory experimentation in the past, though certain efforts have been made to handle them under conditions paralleling their native surroundings, with the object of furthering knowledge concerning nesting habits, parasites, and sex ratios. Fabre's work (1879-1907), particularly with Osmia; Frison's work (1926a) with Bremus; and Rau's work (1924) with Bremus and (1928) with Ceratina will serve as examples of the type to which reference is made. But still less has been done along the lines of experiment with individual bees. An example of this type is the unpublished work of Buchsbaum and Boyer at the University of Chicago, discussed by Allee in "Animal Aggregations" (1931). These workers studied *Melissodes agilis* males in an attempt to determine the relative importance of light and temperature as ecological factors inducing an inactivity which might be variously spoken of as sleep, hibernation, or mere inactivity. They took advantage of the sleeping habits of these bees, collecting them while they were still inactive in early morning on Helianthus, where they were found sometimes in numbers of fifteen to twenty, or even more, upon one flower.

b. Collecting technique.—The actual problem of collecting varies with the bee species or genus, or even family. Each comes to present a separate question of procedure and for efficient work it is necessary to remember or relearn whether the bee will permit approach with vial and cork and will fly up or will drop off the flower, and whether the net must be placed over the flower and time given for the bee to rise from the ground into it, or whether the net must be swung down or up or sideways. Certain species are particularly gifted with the tendency to escape through the net; in this respect, the males are the worst offenders of the sexes. The males of Chloralictus are extremely agile; small Prosopidids and Andrenids are hard to keep; females of *Ceratina dupla* give very much trouble; and males of *Ceratina dupla* are almost impossible to retain in the average net. No straight sweeping has been done. It has been the exceptional bee specimen, in the collection under discussion, that has not been located on the flower and the method of its capture worked out in advance.

Crushing the bee lightly by twisting the net serves as an excellent means of keeping it in place after it has climbed as high up the net as is desired in

its positive response to sunlight. It is then possible to insert the vial or bottle with little danger of the bee's escaping and with little danger of being stung. The collection at hand and the experiments here described have been made with exactly seven stings, each one due to carelessness and over-confidence. The general statement may be made that no bee's sting is prolongedly painful, the female bumblebees being worse than the giant *Xylocopidae* of the tropics.

All bees in the field seem to be photopositive. It has been possible, by judicious maneuvering of the vial, to keep six quite large bees inside while it is uncorked. Any that escape are due to random movements on the part of the bees. It must be added that some of the *Prosopididae,* in particular, are slow to react and they and other bees are inclined to be exploratory in reaction, thus adding additional delay in completing the response to sunlight by climbing up in the vial.

The net must be held over the early *Andrenidae* visiting *Claytonia virginica.* Cutting off the light sends them off the flower to the ground, from which they arise after a minute or so, sometimes having crawled along over the ground and out under the net before coming up. This is particularly true of both sexes of *Ptilandrena erigeniae.* Perhaps a vial over the flower is the safest means if this bee is approached from behind.

Anthophorids can usually be taken right on the flower by covering them with the bottle.

Apis mellifera is best taken with the net; a half dozen in the net can easily be transferred to a vial at one time.

Bombidae are taken easily with a large bottle, or in the net with any kind of sweep.

Ceratinids are almost impossible to take without a side swing of the net and must be transferred to the jar or vial at once. They are easily taken while inside of flowers such as *Pentstemon laevigatus.*

Eucerids are easily taken while on the flowers but the net is safest.

Halictids are individual problems. Often they can be taken with the vial or bottle but some species cannot be so collected.

Some Colletids are taken with the vial or bottle. I have taken some with a vial over the nest entrance.

Prosopidids are best taken with the net if the mesh is small.

All of the *Megachilidae* are easy to take, except *Sayapis* which must often be taken on the wing.

Nomadids, Epeolids, and other inquilines such as *Sphecodes* and *Coelioxys* seem particularly quick in reacting to approach. Many must be taken on the wing.

In general, the males are far more alert than the females and must be taken on the wing much more often.

Bees taken in copula, otherwise alert, are often insensible to being struck by the net and continue in copula on the net.

Melissodes agilis almost convinces one that its females may in some cases seek the males instead of the reverse condition, which usually prevails among bees. At times extreme difficulty has been experienced in collecting one or two females, while males were relatively common and were often found resting on the flowers. At least two females have been seen approaching the males, and one of the resulting pairs was taken in copula.

c. Non-experimental survival in captivity.—Before it was possible to set up the apparatus and begin experiments, a considerable number of bees were successfully brought in to the laboratory and fed honey mixed with glucose, or even glucose alone dissolved in water. Except for the females and large males and workers of the *Bombidae*, all bees were brought home in 6 and 8 dram vials, with a small twig inserted between vial and cork. It was found practically impossible to predict the viability of the temporary inhabitants of any given vial. Any number up to five large, or even twenty small, bees might survive 100% with or without one or more flowers in the vial, or there might be 100% mortality. Neither the species of bee nor the elapsed time between collecting and return to the laboratory had any correlation, in so far as could be determined. This observation may well be borne in mind during consideration of the experimental data. It indicates a variability in the vitality of any group of bees of the same species taken during a day's collecting, which may be indicative in turn of a correlation between "elapsed time since emergence" and "remaining vigor." It seems hard to account otherwise for the fact that bees taken in the morning at nine o'clock may out-live others, apparently larger, of the same species, taken at four o'clock, when both are used in experiments beginning at five-thirty and running for two hours or more.

In some instances, the larger *Bombidae* were brought back in cylindrical cages made of wire screening. These seemed to survive no longer than those brought back in the vials.

It may be well to note that some of the smaller Halictids survived for over six weeks, living two or three females to the vial, and with each being fed a small drop of the honey each day. *Seladonia fasciata* and some of the *Chloralictus* females, particularly *cressonii*, would most amusingly simulate death when their vials were disturbed to insert the card bearing the honey. (This habit is employed in nature where these bees often fall to the ground the instant their flower is disturbed.) In some instances they would show no movement after this reaction, until from fifteen to thirty seconds, or even longer, had elapsed.

Reconsideration of methods employed in collecting these bees to be used for experiment would suggest that such experiments can only be followed

through effectively, where the bee source is very close to the laboratory,—preferably within fifteen minutes or less. All collecting should be done with the vial being inserted over the bee while it is feeding on the flower. The shock of net collecting cannot be overestimated. It was found necessary to employ it in a host of cases but its harmful effects were well recognized. If a conveyer larger than the vials used could be devised, it would undoubtedly give more accurate results, though the problem of removing a desired individual from a group of forty or more bees in a large container may dampen initial enthusiasm for this means of transportation.

Ideally the bees should be raised, and taken for experiment immediately after emergence. This desideratum will scarcely be realized save in the cases of the semi-social bees or the bumblebees.

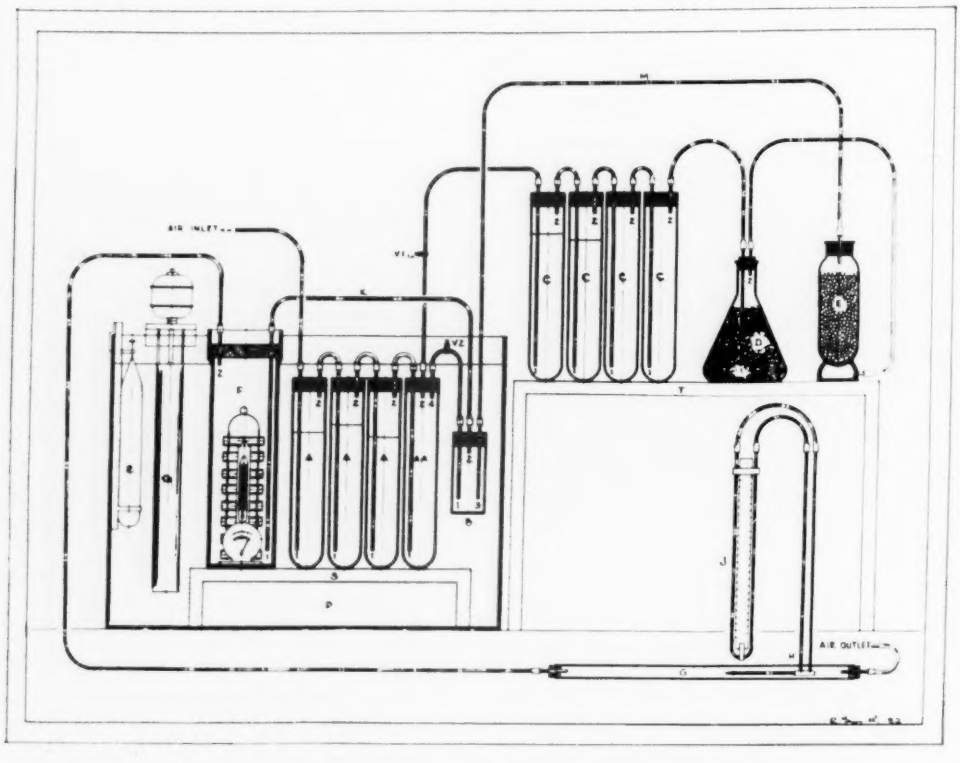

FIG. 1. APPARATUS USED IN TOLERATION EXPERIMENTS

d. Apparatus used in toleration experiments.—The apparatus used in the experiments with grouped and isolated bees of various species, under varying conditions of controlled humidity and temperature, is shown in Figure 1. All the following letters and numbers refer to this figure.

The apparatus consisted essentially of a constant temperature bath P, with circulation device Q and thermostat R, which could be maintained at any desired temperature above room conditions. In this bath are indicated three washing jars, each marked A, one safety jar AA, a mixing jar B, and

the specimen jar F containing also the hair hygrometer and thermometer. Jars A, AA, and F are supported by the rack S in the bottom of the bath. To the right, on an elevated stand, are four sulphuric-acid jars C, two of them serving as safety jars, a fume-removing jar D, and a calcium chloride jar E. Beneath this stand is the Pitot tube H in its brass tube G and with its U-tube-gauge J. The glass vials, open but screened at both ends, which contain the experimental material are shown in their wire rack behind the hair hygrometer in F.

Compressed air in desired quantities is admitted to the first jar marked A, containing tap water, by the tube marked AIR INLET. It passes to the bottom of the jar by the glass tube through the water-tight cork and enters the jar at 1. It is washed and passes out at 2, entering the next jar at 1, is washed a second time and passes out at 2 to enter the third jar for the third washing, only to leave by 2 and enter the safety bottle AA by inlet 1. This bottle serves to collect any surplus water and prevents flooding of the sulphuric-acid bottles in case of a break in the air line.

From jar AA the washed air may leave by two exits controlled by valves V1 and V2. If high humidity is desired, V1 is closed and the saturated air passes at once into jar B by 1 and leaves it by 2 to enter jar F by entrance 1. Circulating upward, this air passes freely through the screened vials and then leaves by 2 to enter the brass tube G where the Pitot tube records its rate of flow as it escapes by the AIR OUTLET.

If dry air is desired, the valve V2 is closed and V1 is opened, all washed air from AA passing at once into the concentrated sulphuric acid of the first C jar by the entrance 1. It leaves by 2 and enters the second jar where there is a second bathing in concentrated sulphuric-acid. The two additional jars marked C are both safety jars, from the last of which the air passes into the flask D by the glass tube leading to the bottom of the flask at 1. This flask contains glass-wool, bone-black, and charcoal, and removes sulphuric-acid fumes. Leaving by the exit 2, the dry air enters the bottom of the jar E containing calcium chloride and passes up through it for a final drying. Returning by tube M, the air enters the mixing jar B by entrance 3, leaves it by exit 2, and then enters the bee-jar F.

If humidities of any type intermediate between maximum dryness or saturation are desired, it is possible to so control valves V1 and V2 that varying proportions of air pass through the water alone and through the sulphuric acid, mixing in jar B as they enter by 1 and 3 and leave by 2. It is to be noted that all air used passes through the washing jars as the first step in its treatment.

Three points concerning this apparatus must be mentioned: First, tests were run using indicators, which showed that there were practically no fumes of sulphuric-acid carried over that could have been suggested as a

factor contributing to the death of the bees. Second, the gauge of the Pitot tube was operated with water and in a manner permitting the recording of the low rates of air flow used in these experiments. To corroborate the methods used, check experiments were run on various rates of air flow, which confirmed the readings obtained by the method used. Third, the hair hygrometer was tested at intervals by wet and dry-bulb thermometer readings under varied conditions of temperature and humidity.

2. Experiments with Isolated Bees under Controlled Conditions.

During the course of the experiments described in this section, air was passed through the container at rates ranging between 5 and 12 liters per minute. The relative humidity is given for each group of experiments, along with the temperature in degrees centigrade. Reference to evaporation rates and relative humidity, as given for the various communities of the dune and morainic series and for prairie by Fuller (1914) (see Table VII this paper), reveals considerable variation between these communities. Fuller's data cover experiments during three seasons, each beginning early in May and running almost through October, though all of the communities were not tested throughout the entire season each year. As indicated in the table, the first part of it shows comparative results for the season, while the second part deals only with the ten weeks from the last of June until the first of Septem-

TABLE VII—*Evaporation rate in certain plant communities as given by Fuller**

Section a. Mean weekly evaporation rates in cc. from a standard atmometer for three seasons under investigation

Association (Community)	1910	1911	1912	Average	Comparative rates
Cottonwood dune (I-3)	21.1	24.6	21.3	22.3	319
Pine dune (I-4)	11.3	10.3	9.7	10.4	149
Oak dune (I-5)	10.3	11.8	10.9	11.0	157
Oak-hickory forest (I-6)	....	9.8	7.8	8.8	126
Beech-maple forest (I-7)	8.1	7.4	5.6	7.0	100
Edaphic prairie (II)	....	12.5	12.5	12.5	179

Section b. Mean weekly evaporation rates in cc. from a standard atmometer during the 10 midsummer weeks of the three years under consideration

Association (Community)	1910	1911	1912	Average	Comparative rates
Cottonwood dune (I-3)	25.0	30.2	20.3	25.2	315
Pine dune (I-4)	14.1	12.6	10.3	12.3	154
Oak dune (I-5)	12.1	13.4	10.1	11.9	149
Oak-hickory forest (I-6)	....	11.6	6.7	9.2	115
Beech-maple forest (I-7)	10.2	8.5	5.3	8.0	100
Edaphic prairie (II)	....	15.1	12.4	13.7	171

*Section (a) is essentially Fuller (1914) Table I. Section (b) is essentially Fuller (1914) Table II.

ber. In the last column of each part of the table, the evaporation rate of beech-maple forest is assigned a value of 100, while the rates for the other communities are calculated from this, for purposes of comparison. It will be noted that cottonwood dune (I-3), pine dune (I-4), and oak dune (I-5) show higher rates of evaporation than do oak-hickory (I-6) and beech-maple (I-7), but that prairie (II) shows a high rate also.

The two sections of the table are included to show that the same general ratio between the different community evaporation rates holds, no matter whether the entire season be considered, or only the ten weeks from the last of June until the first of September.

TABLE VIII—*Averaged survival time and percentage of bees surviving for certain families and genera under conditions of controlled humidity and temperature**

Bees	41° and 25% or less		30° and 25% or less		30° and 60% approx.		41° and 85–100%	
	mins.	% dead	mins.	% dead	mins.	% dead	mins.	% dead
Andrenidae	140	54.5%	...	.....	...	.....	...	.....
Colletidae	185	66.6%	...	.....	185	0.0%	...	.....
Chloralictus	49	66.6%	327	70.3%	54	0.0%	...	.....
					401	33.0%		
Other Halictidae	63	73.5%	330	69.6%	354	22.0%	175	71.4%
					62	0.0%		
Calliopsis	177	85.7%	...	.....	172	0.0%	140	44.4%
					140	0.0%		
Prosopididae	70	71.4%	...	.....	70	0.0%	...	.....
Apidae	65	78.0%	278	75.0%	72	50.0%	...	.....
					317	83.0%		
Bombidae (Bremidae)	145	65.4%	...	.....	300	0.0%	39	50.0%
					39	0.0%		
Ceratinidae	78	57.1%	508	71.4%	78	0.0%	68	100.0%
					288	50.0%		
Melissodes	86	75.0%	208	33.3%	74	50.0%	...	.....
					200	0.0%		
Megachilidae	75	75.0%	563	0.0%	52	0.0%	...	.....
					563	100.0%		

*Centigrade temperature and relative humidity given.

Although the greater part of the readings included by Fuller were made at a height of 20-25 centimeters above the ground, it seems entirely permissible to use them as indicating general community conditions for purposes of comparison.

The experiments, described by the writer in this section, were designed to test the moisture conditions of the communities as possibly exerting a selective effect upon certain species or groups of bees. Bees apparently frequenting prairie should stand low relative humidity more successfully than should bees apparently frequenting the more moist, more humid communities. Otherwise the humidity-evaporation factor cannot be considered vital in attempting to work out bee distribution among the communities.

Table VIII gives averaged data by families and certain genera and is designed to indicate the effects of varying combinations of temperature and humidity upon the same classes of bees. The first set of conditions shows high temperature and low relative humidity. A glance at the table will show that these conditions were most severe. The second combination, with temperature around 30 degrees centigrade but with low relative humidity, reveals longer survival in every case where data are available. The third set of conditions represents, in reality, room conditions, and the data are in fact mostly drawn from controls. Two sets of data are given in a number of cases and it will readily be seen that the bees survived well in comparison with the first two experimental groups. The final column of data is the most incomplete and represents only four families of bees. However, it can be seen that these conditions are apparently more severe than the high temperature and low humidity for *Ceratinidae* and *Bombidae*, but are less severe for certain *Halictidae* and some bees of the genus Calliopsis of the *Panurgidae*. The *Halictidae* as a family show little tendency to restrict their visits to one type of plant community and the species of Calliopsis of the *Panurgidae* is also "general" in its distribution. The *Ceratinidae*, if anything, are found somewhat more commonly in dry conditions, while *Bremus vagans*, the species used in these experiments, apparently frequents the more humid regions, if any decision concerning its distribution is justified. This particular comparison thus offers only partial confirmation of the selective action of the physical factors under consideration.

At this point, it is necessary to call attention to the method of determining survival values for any experiment. Under ordinary conditions, the time of death of each specimen should be recorded and survival values calculated from these results. Under the conditions of the experiments described in this paper, it was necessary to lift the jar F from the bath P (Figure 1) quickly, in order to see if the specimens were dying. It had to be returned before cooling could take place, and it could not be opened and the bees taken out, or the entire conditions of the experiments would have been altered. Furthermore, a motionless bee, even with wings apparently set, would often prove to be alive and capable of revival. Hence it was necessary to wait until such time as a number of the bees were apparently dead, and then remove them and record the condition of each bee.

In Table IX, survival results under conditions of high temperature and low humidity are given for various species and sexes of bees. These bees were isolated individuals, used in comparison with groups of similar species in experiments to be described later (Section V C) and they had to be removed at times suitable for comparison with the grouped bees. Thus their survival percentages were controlled by the general experiment (the method is commented upon in the preceding paragraph), and it was not possible to

TABLE IX—*Data of isolated bees from group-isolated individual experiments of Section V B. Survival time compared with type of habitat. 41° C. and 25 to 0% relative humidity*

Bee	Assigned weight	Sex	No. of experiments	Total bees	% dead	Time out	Calc. mins. 100% dead	Habitat type
Clisodon terminalis	4	♀	1	1	100.0%	28	28	Moist (this region)
Apis mellifera	4	♀	8	41	78.0	62	79	General
Bremus americanorum	2	♀	5	18	63.8	100	157	General
Bremus americanorum	1	♀	1	3	83.3	462	554	General
Bremus americanorum	2	♂	1	1	100.0	81	81	General
Bremus auricomus	2	♀	1	1	100.0	87	87	General (prairie)
Bremus bimaculatus	3	♂	1	1	100.0	116	116	Moist
Bremus fervidus	2	♀	3	3	0.0	140	...	Not Robertson
Bremus fervidus	3	♀	2	7	50.0	142	284	Not Robertson
Bremus fervidus	2	♂	1	1	0.0	120	...	Not Robertson
Bremus separatus	2	♀	3	10	50.0	96	193	General (prairie)
Bremus vagans	3	♀	7	39	81.1	80	98	Moist
Ceratina dupla	6	♀	3	14	53.5	78	145	General (prairie)
Melissodes agilis	5	♂	9	43	76.7	78	102	Dry (prairie)
Melissodes cnici	4	♂	1	4	25.0	126	504	Dry (decidedly prairie)
Melissodes simillima	5	♂	2	4	75.0	75	100	General (prairie)
Melissodes trinodis	4	♂	1	1	100.0	58	58	General (little dune-morainic)
Melissodes vernoniana	4	♀	2	8	87.5	104	119	Dry (prairie)
Melissodes vernoniana	5	♂	1	3	83.3	79	94	Dry (prairie)
Alcidamea simplex	6	♀	1	3	50.0%	40	80	General (prairie)
Osmia distincta	5	♀	1	6	91.6	78	85	General (red-white oak)
Osmia pumila	5	♀	2	4	88.5	59	66	Moist (flood-plain)
Sayapis sayi	4	♀	1	3	67.0	109	123	Dry (prairie)
Xanthosarus latimanus	3	♀	1	1	100.0	70	70	Dry (prairie)
Parandrena andrenoides	5	♀	1	1	87.5	289	330	General (moist)
Pterandrena aliciae	5	♀	2	8	62.5	102	163	General (no dune-morain.)
Colletes eulophi	5	♀	1	5	60.0	135	225	General
Colletes valida	4	♀	1	4	75.0	290	386	Dry (this region)
Agapostemon radiatus	5	♀	1	3	83.3	79	94	General
Agapostemon viridulus	5	♀	4	17	73.5	32	45	General (dry)
Chloralictus coeruleus	6	♀	1	3	67.0	64	96	Moist
Chloralictus coeruleus	6	♀	1	1	100.0	43	43	Moist
Chloralictus sparsus	7	♀	1	4	75.0	45	60	General (flood-plain)
Chloralictus tegularis	7	♀	2	3	87.5	43	49	General
Chloralictus versatus	7	♀	6	26	67.7	47	70	Cosmopolitan
Chloralictus versatus	7	♂	1	3	67.0	36	54	Cosmopolitan
Curtisapis coriacea	5	♀	1	7	71.4	39	54	Moist
Evylaeus arcuatus	7	♀	2	12	58.3	66	113	General
Evylaeus quadrimaculatus	7	♀	1	1	100.0	65	65	General
Evylaeus quadrimaculatus	7	♂	1	5	50.0	65	130	General
Evylaeus truncatus	7	♀	1	2	100.0	75	75	General
Odontalictus ligatus	6	♀	5	24	85.4	56	65	Dry (prairie)
Seladonia fasciata	6	♂	1	3	67.0	86	129	General
Calliopsis andreniformis	6	♀	2	14	82.1	106	129	General
Prosopis ziziae	7	♀	1	7	78.6	70	90	General (dry)

record 100% mortality. To give us a basis of comparison between the different species and sexes, the time of 100% mortality has been calculated for each group, and the time value given affords some indication of the vitality of the bee under consideration. This was, of course, an arbitrary calculation and is presented only to facilitate comparison of survival and the most frequented type of habitat or community for the species. In Table IX, these characteristic habitat types or community types are given in the right-hand column as, for example, "moist" if the bee is apparently adapted to some habitat type, or "general" if no such adaptation is indicated.

In any experiments involving loss of water through evaporation by the animal being studied, the surface-mass ratio would be expected to exert a measurable effect, causing smaller bees to die more rapidly than larger bees. For this reason, the bees that are listed in the experiments described in Tables IX, XI, XIII, and XV are given values corresponding with size, the largest bee having the smallest value or "1," and the smallest bee being given the value "7." These values are approximations. Efforts to determine an exact set of values by weighing the bees were only partially successful. These values appear in the tables mentioned under columns marked "Assigned weight" but they were not considered in any way when determining assumed 100% mortality for the bees.

The descriptions of the habitat "tendencies" of the bees in Table IX may be placed in a series ranging from "moist" through "general with emphasis on moist," "general with emphasis in red-white oak," "general," "general with emphasis on prairie," "general with emphasis on dry," "dry with emphasis on prairie," "dry," and ending with "dry most strikingly prairie." These values are assigned to the bees mainly from study of the Robertson data as applied to Fuller's communities.

If now we summarize the data of Table IX into the habitat characterizations given above, and multiply each assumed 100% death value in minutes by a percentage equal to the "Assigned weight" value of the bee, the results can be compared in Table X.

Reference to the table shows the shortest survival under dry, hot conditions by bees which apparently would be expected to visit mostly conditions which we designate as "moist." The value 31.3 contrasts sharply with the values for "general" visitors which are supposed to visit dry regions or regions of high evaporation more than they do moist regions. These values are 48.2, 42.7, and 42.7. It will also be noted that bees described purely as "general" show a value of 55.4, which is higher than the "moist," "general dry," or "general prairie." This may be explained by crediting these wide-flying "general" visitors with greater all-round vitality and resistance to lethal conditions of all kinds. The last two values are indications of extreme resistance to dryness. "Dry," or 154.4, is given for *Colletes valida,* which was

taken on the dry sand along Lake Michigan, below Zion City, Illinois. These bees burrow 18 to 24 inches through hot, dry sand to build their nests. The second value given, for "general visitor with moist emphasized," 103.5, is far higher than consistency would warrant. However, this includes *Parandrena andrenoides*, a spring bee which has shown the habit of simulating death upon disturbance. It is conceivable that the dryness and heat act as disturbing stimuli which cause this bee to become motionless and reduce metabolism to a very minimum. It is inconceivable that death simulation should be accompanied by higher metabolic rate than that of the terrific vivacity of an active bee. This must still be tested, however.

TABLE X—*Averaged survival values, weighted for bee size, compared by characterizations of the communities the bees most frequent**

Habitat type or characteristics of habitat or habitats frequented	Averaged weighted minute-value for bees considered	Number of sexes and species included	Number of bees included	Number of experiments included
Moist	31.3	7	56	14
General (moist emphasized)	103.5	2	8	2
General (red-white oak emphasized)	42.5	1	6	1
General	55.4	17	149	37
General (prairie emphasized)	48.2	5	32	10
General (dry regions emphasized)	42.7	2	24	5
Dry (prairie emphasized)	42.7	6	82	19
Dry	154.4	1	4	1
Dry (decidedly prairie)	201.6	1	4	1
Total	....	42	365	....

*Data from Table IX. 41° C. and 25 to 0% relative humidity.

With study of the survival data of these bees by genera or families, and making no correction for size, it is observed that the males and workers of Bremus show a correlation in survival with habitat indicated: "moist" is 107 minutes, "general" is 119 minutes, and "general (prairie)" is 140 minutes. (Data averaged from Table IX.)

The five groups of data dealing with the family Megachilidae give "moist," 66 minutes; "general (red-white oak)," 85 minutes; "general (prairie)," 80 minutes; and "dry (prairie)," 96 minutes. This correlation is quite close when the wide variety of genera is recognized, Alcidamea, Osmia, Sayapis, and Xanthosarus being included.

Among the sexes and species of Melissodes, "general" has a value of 58 minutes; "general (prairie)," of 100; "dry (prairie)," of 105 minutes; and "dry (decidedly prairie)," of 504, due to the sturdy *Melissodes enici*. This group gives perfect correlation.

In the Andrenidae, the long-lived *Parandrena andrenoides* outlived the fall *Pterandrena aliciae* 330 to 163 minutes, though the former is "general

(moist)" and the latter "general." *Parandrena andrenoides* was mentioned above.

When reference is made to Chloralictus, the toleration data appear to show a negative correlation with habitat, "moist" being 69; "general (flood-plain)," 60; and "general," 58. However, these bees are so small that rapid drying out must in practice hide any physiological adaptation that might exist. If this explanation would not suffice, the death simulation of Chloralictus could be invoked to urge an uninterrupted activity on the part of the bees that visit both dry and moist environments, but a cessation of activity on the part of the moist-habitat bees when introduced into the unnatural dry conditions of the experiments. Given equal vitality, the difference in metabolism would explain the difference in survival time. I am inclined to favor the size explanation.

Among the remaining bees of the family *Halictidae*, the data do not correlate with the habitats. "Dry (prairie)" shows 65 minutes, "general (dry)" shows 45 minutes, "general" shows 101, and "moist" shows 54 minutes. Among the *Halictidae*, it would seem best to explain this lack of correlation with the habitat by the hardiness and vigor of the "general" bees. In this group, as in the genus Chloralictus, however, small size with attendant rapid evaporation to a lethal point might act to mask any physiological adaptation.

The two species of Colletes considered are well correlated in survival with their habitats. C. valida, "dry," shows 356 minutes while *C. eulophi*, "general," is 225 minutes.

In Table XI are presented data of individual experiments with isolated bees, made separately from the experiments with groups and isolated bees reported in Table IX. In these experiments, a minimum and a maximum death value is given for each bee, which means that the bee was alive at the first time and dead at the second. For all values used, the mid-time is calculated. Weighing these data for bee size, as indicated in the table and as done in Table IX, we can summarize the values as shown in Table XII.

Among these experiments, bees with a "moist" habitat show the lowest survival value or 15.1, while "general" is only 15.5. The difference is much less than that between the same bee types of Table X, where the values are "moist" 31.3 and "general" 103.5. However, all the "more dry" habitats show higher values [though the "dry (prairie)" is only 20.5] with the exception of the last value, 9.6, which was obtained from a bee undoubtedly injured. Those of this species, *Melissodes cnici*, gave very high values in the earlier table.

Thus it would seem that bees under experimental conditions of high temperature and low relative humidity show evidences of correlation in length of survival with conditions of the habitat which they most frequent.

But survival data taken from bees under conditions of approximately 30

TABLE XI—*Survival tests of odd bees at 41° C. and 25 to 0% relative humidity*

Bee	Assigned weight	Sex	Life Minimum Mins.	Mid Mins.	Life Maximum Mins.	Habitat most frequented
Clisodon terminalis....	4	♂	17	24	31	Moist (this region)
Clisodon terminalis....	4	♂	31	37	44	Moist (this region)
Bremus vagans.....	3	♀	17	24	31	Moist
Bremus vagans.....	3	♀	0	8	17	Moist
Melissodes bimaculata.	4	♂	31	37	44	General (prairie)
Melissodes bimaculata.	4	♀	100	100	100	General (prairie)
Melissodes bimaculata.	4	♀	108	113	119	General (prairie)
Melissodes cnici.....	4	♂	17	24	31	Dry (decidedly prairie)
Melissodes simillima...	5	♂	12	20	29	General (prairie)
Melissodes trinodis....	4	♂	31	37	44	General (little dune-morainic)
Coelioxys sayi.....	5	♂	82	82	82	General (dry)
Coelioxys sayi.....	5	♂	98	103	108	General (dry)
Coelioxys sayi.....	5	♂	0	4	9	General (dry)
Megachile generosa....	5	♂	21	27	34	Dry (dune and prairie)
Sayapis pugnata.....	4	♀	77	83	89	Dry
Sayapis sayi.....	4	♂	108	113	119	Dry (prairie)
Sayapis sayi.....	4	♂	66	72	79	Dry (prairie)
Xanthosarus latimanus.	3	♀	22	27	33	Dry (prairie)
Xanthosarus latimanus.	3	♀	22	27	33	Dry (prairie)
Xanthosarus latimanus.	3	♀	33	45	58	Dry (prairie)
Pterandrena aliciae....	5	♀	34	42	50	General (no dune-morain.)
Curtisapis coriacea....	5	♀	22	27	33	Moist
Curtisapis coriacea....	5	♀	33	45	58	Moist
Curtisapis coriacea....	5	♂	66	72	79	Moist
Halictus lerouxii.....	5	♀	12	20	29	General
Odontalictus ligatus ...	6	♂	50	58	66	Dry (prairie)
Odontalictus ligatus ...	6	♂	17	24	31	Dry (prairie)
Odontalictus ligatus ...	6	♀	12	20	29	Dry (prairie)
Oxystoglossa confusa ..	6	♀	21	27	34	General

TABLE XII—*Averaged survival values, weighted for bee size, compared by characterizations of the communities the bees most frequent**

Habitat type or characteristics of habitat or habitats frequented	Average weighted minute-value for bees considered	Number of bees
Moist	15.1	7
General	15.5	4
General (prairie)	27.5	4
General (dry)	31.5	3
Dry	23.3	2
Dry (prairie)	20.5	8
Dry (decidedly prairie)	9.6	1
Total	....	29

*Data from Table XI. 41° C. and 25 to 0% relative humidity.

TABLE XIII—*Data of isolated bees from group-isolated individual experiments of Section V B.* Survival time compared with type of habitat*

Bee	Assigned weight	Sex	No. of experiments	Total bees	% dead	Time out	Calc. mins. 100% dead	Habitat type
Apis mellifera	4	♀	6	40	75.0%	46	61	General
Ceratina dupla	6	♀	1	7	71.4	508	611	General (prairie)
Melissodes vernoniana	4	♀	2	9	33.3	200	600	Dry (prairie)
Agapostemon viridulus	5	♀	2	10	50.0	307	614	General (dry)
Chloralictus sparsus	7	♀	1	1	100.0	236	236	General (flood-plain)
Chloralictus sparsus	7	♂	1	6	83.3	742	890	General (flood-plain)
Chloralictus versatus	7	♀	1	6	66.6	236	354	Cosmopolitan
Chloralictus vierecki	7	♀	1	5	80.0	323	404	Dry (this area)
Chloralictus zephyrus	7	♀	2	6	66.6	137	205	General (moist)
Curtisapis coriacea	5	♀	1	5	60.0	307	510	Moist
Dialictus anomalus	7	♀	1	1	0.0	124	157	Dry (prairie)
Evylaeus arcuatus	7	♀	1	5	100.0	615	615	General
Oxystoglossa confusa	6	♂	1	3	100.0	116	116	General

*30° C. and 25 to 0% relative humidity.

TABLE XIV—*Averaged survival values, weighted for bee size, compared by characterizations of the communities the bees most frequent**

Habitat type or characteristics of habitat or habitats frequented	Averaged weighted minute–value for bees considered	Number of sexes and species included	Number of bees included	Number of experiments included
Moist	255.0	1	5	1
General (moist)	310.5	3	13	4
General	193.1	4	54	9
General (prairie)	366.6	1	7	1
General (dry)	307.0	1	10	2
Dry (prairie)	174.9	2	10	3
Dry	282.8	1	5	1
Total	.....	13	104	....

*Data from Table XIII. 30° C. and 25 to 0% relative humidity.

degrees centigrade and low relative humidity show little correlation with habitat conditions. There is the increased average length of survival which is to be expected. The data are presented in Table XIII, and the weighted, averaged values for the different habitats are given in Table XIV.

The majority of these experiments were with bees belonging to *Halictidae* in which group there was shown to be least correlation between survival time and habitat. These data would seem to indicate the difficulty of establishing any clean-cut correlation between survival and relative humidity of

the habitat of *Halictidae*, particularly where the temperature is not lethal in the experiments.

The specimens of *Apis mellifera* used here, in their behavior, indicate sensitivity to humidity on the part of these bees, to an unexpected degree. It will be seen that they died more rapidly than any others, and sufficient numbers of them were used to give a fair test. It must be noted, however, that this bee seems the least able of any species taken to endure laboratory experimental conditions.

Additional single records at 30 degrees centigrade and low relative humidity are available but offer no usable data except a general confirmation of longer survival if the temperature is reduced. These records are given in Table XV.

At a temperature of 30 degrees centigrade and with low relative humidity, it was observed that three males of *Oxystoglossa confusa* were dead in 116 minutes. The bee is predicted as "general." At the end of 732 minutes only 80% or four of another group of the same sex and species were dead when the temperature had been the same and the relative humidity had been 60%. Yet when the temperature was 33 degrees centigrade and the humidity was low, three females were all found to be dead in 58 minutes. If these bees were as adaptable as their flower-visiting habitats would indicate, no such variation of survival with humidity change should take place. Possibly there is no correlation between habitat and survival in this species of *Halictidae*.

Apis mellifera workers were indicated as "general" and showed low survival under conditions of either high or normal temperature and low relative humidity. But with temperature at 27 degrees centigrade and 85% or higher relative humidity, 85.7% of 7 isolated bees were still alive after 375 minutes. Another "general" bee with a differential survival!

Ceratina dupla, given as a "general" bee, with some emphasis on prairie visits, showed 53.5% survival among 14 bees after an hour and 18 minutes at 41 degrees centigrade and low relative humidity but showed 100% dead from a group of 3 after 1 hour and 8 minutes at 41 degrees centigrade and maximum relative humidity. This would seem to show a physiological correlation with a more dry environment.

Comparing three types of experiment using *Agapostemon viridulus*, given as "general" with emphasis on "dry" visits, we observe the following:

(1) 4 exps., temp. 41°C., rel. hum. low, 17 bees, 73.5% dead, 32 mins.
(2) 2 exps., temp. 30°C., rel. hum. low, 10 bees, 50.0% dead, 307 mins.
(3) 1 exp., temp. 41°C., rel. hum. very high, 5 bees, 80.0% dead, 211 mins.

According to the survival data, this bee would seem to be adapted to moist conditions, although the observational data and our predictions would make it "general" or with a tendency toward dry conditions.

Calliopsis andreniformis is given as a bee visiting all habitats. But with 41 degrees centigrade and low relative humidity, 82.1% of 14 bees were dead in 106 minutes, while with the same temperature and with the relative humidity at maximum, all of a set of 5 isolated bees were still alive after 140 minutes. But the above were all females. Four males at that temperature and with high humidity were all dead in 140 minutes. Apparently a variation in resistance of the sexes is indicated.

Bremus vagans is given as a bee frequenting moist habitats. Using 41 degrees centigrade as the temperature in all cases, we observe that of 39 specimens under very dry conditions, 81.1% were dead in 80 minutes. Yet with relative humidity practically at saturation, with 8 bees used, 50.0% were dead in 39 minutes. This again would not be evidence in favor of a correlation between conditions of habitats most frequented and maximum experimental survival conditions.

TABLE XV—*Survival tests of odd bees at 30° C. and 25 to 0% relative humidity*

Bee	Assigned weight	Sex	Life Minimum Mins.	Mid Mins.	Life Maximum Mins.	Habitat most frequented
Melissodes bimaculata	4	♀	0	27	55	General (Prairie)
Megachile generosa	5	♂	55	167	280	Dry (dune and prairie)
Megachile generosa	5	♂	55	167	280	Dry (dune and prairie)
Megachile generosa	5	♂	55	167	280	Dry (dune and prairie)
Megachile mendica	4	♀	55	167	280	General (cosmopolitan)
Sayapis pugnata	4	♀	176	182	189	Dry
Sayapis pugnata	4	♀	189	201	214	Dry
Sayapis pugnata	4	♀	189	201	214	Dry
Sayapis sayi	4	♂	238	...	...	Dry (prairie)
Xanthosarus latimanus	3	♂	208	223	238	Dry (prairie)
Xanthosarus latimanus	3	♂	238	...	...	Dry (prairie)
Xanthosarus latimanus	3	♀	0	7	15	Dry (prairie)
Evylaeus arcuatus	7	♀	114	130	147	General
Evylaeus arcuatus	7	♀	114	130	147	General
Evylaeus arcuatus	7	♀	290	...	...	General
Evylaeus arcuatus	7	♀	290	...	...	General
Evylaeus arcuatus	7	♀	147	163	180	General
Evylaeus arcuatus	7	♀	223	256	290	General
Evylaeus truncatus	7	♀	114	130	147	General
Evylaeus truncatus	7	♀	147	163	180	General

3. Factors Influencing Experimental Results.

During the course of the description of experiments, it has been necessary to mention several influencing or qualifying factors. The simulation of death is one factor that may be disputed. I have observed it so frequently among the *Halictidae* and the *Andrenidae* that the only question need be its efficacy in the present instance. This would depend upon duration of the simulation period. In the case of a mechanical shock such as is responsible most often for inducing the reaction, it was observed that if the shock be re-

peated at intervals, there was some but very little adjustment to it. Successive periods of inactivity apparently became somewhat shorter, but really very little shorter. Whether heat and low humidity could serve as the same stimulus as a mechanical shock is questionable. The nature of the constant temperature bath, in which the bees were immersed in their container, was such that all direct light was eliminated and upon removal the emergence into bright light usually served to stir up the more active bees. It would scarcely seem justifiable to assign more than a few moments to the death-simulation factor as effective in quieting *Halictidae*.

That the high temperature and low humidity exerted a far more rapid lethal effect on small bees than on large bees was evident. Often great difficulty was experienced in pinning Chloralictus or Prosopis specimens that had been killed at high temperature and low relative humidity. They are both small bees and they would actually be brittle in a surprisingly short time. It was usually possible to estimate which bee died first in some of the experiments with groups, reported in the next section. The longer the bee had been dead, the more the difficulty that was experienced in pinning it.

Size of individual containers for the bees was shown to have an effect. This will be discussed later.

One factor that came up before the experiments were undertaken must now be mentioned. With recent work that has been done concerning animal aggregations in mind, the question was raised whether one was justified in treating experiments with isolated individuals of social and semi-social bees in the same manner as one would treat such experiments with solitary or non-social bees. It was decided to test this question along with the survival data. Justification of the methods used in the experiments given in this section is made in the following section, devoted to comparison of reactions of groups and isolated individuals of different bees.

4. Conclusion.

In concluding this section, I would say that there is evidence that certain species of bees tend to visit certain environments or plant community types to an excess over other communities, such that they can be deemed adapted to these communities. It would seem that, in certain of these instances, the fundamental adaptation has been one of the bee to the flowers of those communities, but there is no evidence to prove that the flower adaptation may not be the one which is secondary.

Furthermore, it would seem that certain of these bees which are not apparently more frequent visitors to one community than to another, and which are found in several habitats with all types of relative humidity and with varying evaporation rates, are the more hardy bees and can stand, for longer periods, extremes of temperature or relative humidity. On the other hand, there is evidence that certain species and groups of bees are very definitely

correlated in physiological make-up with the physical conditions of certain plant communities, so much so that, for example, they show more ability to endure dry conditions if they are bees that visit dry communities more often than moist. Conversely, those visiting moist more than dry have less ability to withstand dry conditions. Certain supposedly "general" bees under experimental conditions show an adaptation to one or the other extreme of humidity. (See experiments given later, dealing with groups and isolated individuals.)

The smaller the bee, the less its adjustment, and the less chance of testing such adjustment as it may have.

V. TESTING TOLERATION DATA BY EXPERIMENTS WITH GROUPED AND ISOLATED BEES

A. Animal Aggregations Studies and Their Implications With Respect to the Bee Experiments

A complete study of the subject of Animal Aggregations, together with a very complete survey of the literature, is given by Allee (1931). The bees rank as most interesting material for such studies, exhibiting as they do various degrees of aggregation in different families, genera, and species, from the most solitary species of inquiline to the perfect colony of Apis.

Doubtless several factors have been responsible for the evolution of the well-developed social organization to be seen in the hive bee or even in the Bremidae. The development of the specialized worker class is in all probability a product of this colonial organization and is not one of the factors in its formation.

Just as other more simple animal groupings have come under intensified scrutiny in search of these factors which have been responsible for the aggregating of the individuals composing them, so it should be possible to determine the causes of bee colony evolution. And just as the advantages to be gained by individuals of a simple aggregation of animals have been most carefully sought, so it should be possible to determine the advantages to be gained by aggregations of a more complex nature, such as are exemplified by the colonies of Apis, Bremus, Trigona, and Melipona.

Comparisons of reactions of these colonial forms of bees with reactions under similar conditions by bee species of lower colonial or social organization, or with bees having essentially no tendency toward aggregation, when both groups are exposed to various controlled conditions, should throw some light on the influence of those factors or upon the physiological adaptations of the solitary and social bees to solitary or social life.

The following sections offer some clues toward an eventual solution of the causes and advantages of social organization among the bees, treating

though they do only of heat and humidity, with no discussion of the more general social problems (such as those which center about food, for example) and all of their ramifications into the field of "the division of labor."

B. Is There a Differential Toleration Between Grouped and Isolated Bees Depending Upon the Degree of Sociability of the Species Under Consideration?

Consideration of the general work in the Aggregations field, described by Allee (1931) in connection with the various degrees of colonial integration shown by the bees as a super-family, raises a rather interesting question, which is given as the heading for this section, with regard to bee survival under lethal conditions.

This question can be best discussed by citing certain experimental conditions and then discussing possible results that might be expected from experiments run under those conditions.

If we assume the presence of the lethal conditions of high temperature and low relative humidity, our discussion will center about the humidity factor, the bees being assumed to have little control, under experimental conditions, of the temperature factor which we introduce merely to shorten the life-period for all species under experimentation.

Social or semi-social bees, introduced into these lethal conditions and in vials of what we may call "medium" size with both ends open, permitting free air flow, are placed in groups and are isolated. If five bees form the group, five isolated bees occupy five vials of similar size under identical conditions. The bees of the group, due to their social behavior patterns, might then be expected to attempt to block the flow of dry air through the container, by massing in an effective manner. The isolated bees, thrown upon their own resources and with no aid from other individuals, are unable to simulate the moist conditions of the nest or even to approach those conditions and soon lose water to a lethal point, usually much earlier than the individuals of the group. Furthermore, we may assume that the grouped bees find themselves in a normal environment, as far as the presence of their fellows is concerned, and are hence inclined to become quiet after completing the partial blocking of the air flow. The isolated social or semi-social bee has the further adverse stimulus of being separated from its fellows and may be moved to tremendously exhausting efforts.

It is conceivable, of course, that if the ratio between bee size and vial size is too great in the case of the grouped bees, they will be unable to block the air flow and will continue vain activity in this direction with a resulting diminution of the remaining period of life of each bee. In this case, the isolated bees might even be expected to outlive the grouped bees.

Conversely, if the bees of the group are placed in a vial which is too small,

they will tend to suffocate and the isolated specimens would be expected to outlive the group. Here too the physical factors would completely mask any social behavior patterns, as far as results are concerned.

If we now consider similar experiments with non-social or solitary bees, we may assume that a group of them, placed in the same vial, will exhibit no concerted effort to gain control of the environment. They will naturally profit from the surface-mass ratio in comparison with the isolated bees and will lose less water per bee merely from being together in the one vial. But on the other side, they will often be stimulated to violent activity when they come into contact with each other, as was continually observed in the cases of such bees being brought in from the field, in groups, in vials. The isolated bees may soon settle down to general inactivity, which observation alone, in the case of bees, is capable of assuring us must mean lower metabolic rate than the terrific activity of a bee under some adverse stimulus. Thus the isolated solitary bees may be expected to actually outlive the groups about as often as the groups of bees outlive them.

It might be well to visualize suggested effects of the experimental physical conditions upon the bees in the following manner: Let us assign a value of 7 arbitrarily to any bee which is permitted to live in theoretical, controlled conditions, uninfluenced by physical conditions or presence or absence of other bees. This 7 represents what we may call "remaining life expectancy." Now let us designate social or semi-social bees with "S" and non-social bees with "N." And let us designate bees of any kind in groups as "G" and isolated bees of any kind as "I." Now let us arbitrarily indicate two adverse stimuli: the one the effect of the dry air, which we can designate as 2; the other any adverse stimulus from the presence or absence of other bees, which we may designate as 1. On the other hand, we may designate as 1 the advantage to be gained from the mere physical presence of a group, due to the surface-mass effect.

Then we have "SG" 7, less 2 (air), plus 1 (group effect), and the result is "SG" 6.

And we have "SI" 7, less 2 (air), less 1 (absence of others), and the result is "SI" 4. Which means that if we have a group effect and a social effect the grouped social bees will outlive the isolated ones.

Then too we have "NG" 7, less 2 (air), plus 1 (group effect), less 1 (presence of others), and the result is "NG" 5.

And we have "NI" 7, less 2 (air), and the result is "NI" 5. Which would mean that we might obtain no definite result in either direction as far as experiments with groups and isolated non-social bees are concerned.

C. Survival Experiments Contrasting Groups and Isolated Bees

Using the apparatus described in Section IV C 1 d, experiments were run with intent to compare the survival of grouped and isolated bees of various

species. In so far as possible, the attempt was made to use bees of the same species in a given experiment. Occasionally later study proved that two or more species and even sexes had been used. In certain cases it was known that more than one species, or caste, or sex were being used. In these cases, bees of the different kinds were as far as possible equally distributed between the groups and the isolated individuals.

As indicated in Section V B, the writer must confess to having had certain definite ideas concerning the manner in which the survivals would work out before the experiments were run. Thus it was believed that possibly the groups of *Apis mellifera* would outlive the isolated bees, and it was deemed possible that this would hold for the Bremidae. As a consequence, where any choice was possible between individual bees of the same species, the stronger or more active individuals were placed where conceivably they would live the shortest time. This may have had some slight influence on the general results, although it has been found by these experiments that observation of activity and apparent vitality is a very poor index of longevity or survival.

Over 1,350 bees were used in these experiments and as controls. Only part of these are here reported.

TABLE XVI—*Comparative survival time of grouped and isolated Apis**

Exp. No.	Time		Group			Isolated bees			Survival of *group* over *isolated bees*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
13	1	2	5	5	0	5	4	1	−1
16	1	2	7	4	3	7	7	0	3
69	..	57	5	0	5	5	5	0	5
70	1	33	5	3	2	5	5	0	2
74	..	39	4	2	2	4	4	0	2
80	..	28	5	0	5	5	1	4	1
82	1	23	5	0	5	5	3	2	3
84	1	35	5	4	1	5	3	2	−1
Total	..	..	41	..	..	41	..	..	14

By Student's method of testing for significance there are 468 chances in 10,000 of random sampling giving the same result.

*Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12, vials 1.8 cms. diameter inside by 5 to 6.5 cms. long, designated as "medium."

The results presented in Table XVI are from experiments with workers of *Apis mellifera*, which were exposed to a temperature of 41°C., and 25 to 0% relative humidity, in vials open at both ends but screened, vial dimensions 1.8 cms. inside diameter and 5 to 6.5 cms. long.

The first experiments using Bremus (Bombus) gave results favoring the isolated bees. The conditions of the experiments were essentially similar to those in the preceding table. The results are given in Table XVIIa. Larger containers were then used, and the results were shown to be more favorable to the grouped bees (see Table XVIIb for these data). The vial size in the

second group of experiments with Bremus was increased to 4.5 cms. in diameter and 6.0 cms. long. Since this genus is made up of bees averaging much larger in size than Apis, it was obvious that the grouped bees might well be smothering in the small vials.

TABLE XVII—*Comparative survival time of grouped and isolated specimens of Bremus*

Section a. "Medium"-sized vials*

Exp. No.	Time		Group			Isolated bees			Survival of *isolated bees* over *group*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
3	8	4	3	3	0	3	2	1	1
54	2	0	8	8	0	8	4	4	4
59	1	21	5	4	1	6	3	3	2
65	1	56	6	5	1	6	5	1	0
75	2	29	5	1	4	5	2	3	−1
76	2	29	3	2	1	3	1	2	1
Total	..	..	30	..	..	30	..	..	7

By Student's method of testing for significance there are 1602 chances in 10,000 of random sampling giving the same result.

Section b. "Large"-sized vials†

Exp. No.	Time		Group			Isolated bees			Survival of *group* over *isolated bees*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
96	2	6	5	3	2	5	5	0	2
98	2	6	5	4	1	5	4	1	0
100	1	1	5	2	3	5	4	1	2
101	2	10	5	4	1	5	5	0	1
105	2	0	5	1	4	5	4	1	3
106	1	27	5	4	1	5	3	2	−1
110	3	16	5	2	3	5	2	3	0
111	2	0	5	2	3	5	2	3	0
112	1	55	5	2	3	5	4	1	2
113	2	25	5	3	2	5	3	2	0
Total	..	..	50	..	..	50	..	..	9

By Student's method of testing for significance there are 244 chances in 10,000 of random sampling giving the same result.

*Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12, vials 1.8 cms. diameter inside by 5 to 6.5 cms. long, designated as "medium."

†Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12, vials 4.5 cms. inside diameter by 6.0 cms. long, designated as "large."

The first experiments with Chloralictus were tested in "medium"-sized vials and gave results favoring the isolated bees, as shown in Table XVIIIa. Inasmuch as experiments with others of the *Halictidae* favored the grouped bees, these results were unexpected. A change to smaller vials was made and the results when vials .4 cms. in diameter by 4.0 cms. long were used are shown in Table XVIIIb, favoring the groups. The small bees of the group

were apparently unable to gain control of the vial if it was too large. When the size of the vial was reduced, they were able to exert a combined effort and lessen the harmful effects of the environment.

TABLE XVIII—*Comparative survival time of grouped and isolated Chloralictus*

Section a. "Medium"-sized vials*

Exp. No.	Time		Group			Isolated bees			Survival of *isolated bees* over *group*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
7	1	20	4	4	0	4	4	0	0
8	..	23	6	3	3	6	2	4	1
12	..	45	5	3	2	5	3	2	0
35	..	49	4	4	0	4	4	0	0
38	..	36	3	3	0	3	2	1	1
39	..	48	5	4	1	5	5	0	-1
57	1	4	3	0	3	3	2	1	-2
85†	1	5	5	5	0	5	1	4	4
Total	..	..	35	..	..	35	..	..	3

By Student's method of testing for significance there are 5674 chances in 10,000 of random sampling giving the same result.

Section b. "Small"-sized vials**

Exp. No.	Time		Group			Isolated bees			Survival of *groups* over *isolated bees*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
99	..	52	4	2	2	4	2	2	0
102	..	43	5	3	2	5	5	0	2
103††	1	5	5	3	2	5	4	1	1
104	..	35	4	1	3	4	3	1	2
107	..	50	5	4	1	5	3	2	-1
108	..	41	5	3	2	5	4	1	1
109	..	40	4	3	1	4	2	1	0
Total	..	..	32	..	..	32	..	..	5

By Student's method of testing for significance there are 1422 chances in 10,000 of random sampling giving the same result.

*Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12.
†Some bees of experiment 85 were small species of Evylaeus, a related genus.
**Conditions the same as in Section (a), but the vials .4 cms. diameter by 4.0 cms. long.
††Some bees of experiment 103 were small species of Evylaeus, a related genus.

Studies on species of the larger genera of Halictidae such as Odontalictus and Evylaeus gave a striking difference in survival of grouped individuals compared with isolated individuals (see Table XIX). The physical conditions of the experiments were the same as in those previously reported, and the "medium"-sized vials were used.

The *Halictidae*, which of course include Chloralictus, may be considered semi-social bees, though there are certain notable exceptions. If they are considered as semi-social, then it is to be seen that the above data would indicate that they are reacting in a manner similar to that of the truly social *Apidae* and *Bremidae (Bombidae)*, and are showing group survival for longer periods than the survival of isolated bees under conditions otherwise similar.

A number of experiments were tested at room temperature, approximately 30 degrees centigrade and 20 to 0% relative humidity. Only with *Apis mellifera* were there sufficient cases to record, and they again showed a higher group survival, as reported in Table XX.

TABLE XIX—*Comparative survival time of grouped and isolated specimens of genera of Halictidae, no specimens of Chloralictus included**

Exp. No.	Time		Group			Isolated bees			Survival of *groups* over *isolated bees*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
4	1	40	4	1	3	4	4	0	3
5	1	19	3	1	2	3	2	1	1
6	1	26	3	0	3	3	1	2	1
10	..	39	7	1	6	7	4	3	3
14	..	55	4	2	2	4	4	0	2
15	..	30	4	2	2	4	4	0	2
18	..	57	7	2	5	7	4	3	2
30	..	38	2	1	1	2	2	0	1
32	1	24	7	4	3	7	6	1	2
34	1	15	7	3	4	7	3	4	0
55	..	50	7	5	2	7	5	2	0
56	1	4	3	1	2	3	3	0	2
66	..	55	5	2	3	5	5	0	3
67	1	12	5	5	0	5	3	2	−2
Total	..	..	68	..	..	68	..	..	20

By Student's method of testing for significance there are 22 chances in 10,000 of random sampling giving the same result.

*Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12, vials 1.8 cms. inside diameter by 5.0 to 6.5 cms. long, designated as "medium."

Study of Tables XVI to XX indicates that, if the proper vial-size bee-size ratio is determined upon, groups of social or semi-social bees will outlive isolated specimens. Tables XVIIa and XVIIIa both give data with bees tested in the medium-sized vials which were found successful for Apis and Halictidae other than Chloralictus. These vials evidently proved too large for specimens of Chloralictus to control, and too small for Bremus. As shown in the Tables XVIIa and XVIIIa, the isolated bees outlived the grouped bees in these tests. However, when the vial size was decreased for Chloralictus, as reported in Table XVIIIb, results favored the grouped bees. When the size of the containers was enlarged for Bremus, the group outlived the isolated bees, as shown in Table XVIIIb.

TABLE XX—*Comparative survival time of grouped and isolated specimens of Apis**

Exp. No.	Time		Group			Isolated bees			Survival of *groups* over *isolated bees*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
40	3	40	7	1	6	7	2	5	1
44	5	35	7	5	2	7	6	1	1
48	6	36	7	4	3	7	7	0	3
49	7	5	7	2	5	7	5	2	3
51	3	45	7	5	2	7	6	1	1
52	1	10	5	2	3	5	4	1	2
Total	..	..	40	..	..	40	..	..	11

By Student's method of testing for significance there are 60 chances in 10,000 of random sampling giving the same result.

*Temperature approximately 30° C., relative humidity 20 to 0%, air liters per minute 5 to 12, vials 1.8 cms. inside diameter by 5 to 6.5 cms. long, designated as "medium."

The data given in Tables XVI to XX confirm the suggestions advanced in Section V B concerning the behavior of social or semi-social bees under experimental lethal conditions of temperature and humidity.

In contrast with the experiments described in the preceding Tables XVI to XX, inclusive, which deal with social and semi-social bees, Table XXI presents data obtained from experiments with solitary bees of the family *Euceridae*, genus Melissodes. These experiments were carried on with the bees in vials 1.8 cms. in diameter and 5 to 6.5 cms. long. They were maintained at a temperature of 41°C., and 25 to 0% relative humidity.

Inspection of the data given in Table XXI indicates that the grouped and isolated bees have approximately the same survival time. However, the ex-

TABLE XXI—*Comparative survival time of grouped and isolated Melissodes**

Exp. No.	Time		Group			Isolated bees			Survival of *isolated bees* over *groups*
	Hr.	Min.	Total	Dead	Alive	Total	Dead	Alive	
26	1	11	2	1	1	2	1	1	0
28	2	38	3	2	1	3	2	1	0
29	1	19	5	3	2	5	3	2	0
33	1	10	5	4	1	5	4	1	0
87	1	39	5	4	1	5	4	1	0
88	1	39	5	5	0	5	4	1	1
89	1	39	5	4	1	5	5	0	−1
90	1	12	5	3	2	5	2	3	1
91	1	12	5	4	1	5	5	0	−1
92	1	12	5	3	2	5	5	0	−2
93	1	5	5	5	0	5	5	0	0
94	1	5	5	4	1	5	3	2	1
95	1	5	5	3	2	5	4	1	−1
97	2	6	4	3	1	4	1	3	2
Total	..	..	64	..	..	64	..	..	0

*Temperature 41° C., relative humidity 25 to 0%, air liters per minute 5 to 12, vials 1.8 cms. diameter inside by 5 to 6.5 cms. long, designated as "medium."

periments were not as complete as those reported in Tables XVI to XX which give results obtained from social and semi-social bees. Only one vial size, that one designated as "medium," was used. It would possibly be desirable to test these solitary bees in vials of other sizes. However, "medium" vials were used with the Apis and statistically significant results were obtained, as shown in Tables XVI and XX. Melissodes should have experienced no difficulty, when placed in groups in these vials, that Apis would not have experienced, for the bees are of approximately the same size, both groups having been given an "assigned weight value" of 4, as shown in Table IX, for example.

A study of the data in Tables XVI to XX, inclusive, would seem to indicate that there is some foundation for the belief that social or semi-social bees have developed an adaptation to group existence which acts as an advantage when groups are placed under adverse conditions. If these general results can be shown to hold for all kinds of bees, non-social as well as semi-social and social, then a physical explanation can be sought and one is easily found. The mere physical presence of several bees in one container will reduce the rate of evaporation from each bee, and will permit the bees of the group to live for a longer time, before sufficient water is evaporated from them to cause death, than would be the case with the isolated bees.

However, such a simple mass relation is not the only possibility. Preliminary observations indicate that there is a difference in activity of grouped and isolated social or semi-social bees from that shown by grouped and isolated solitary bees under similar conditions of confinement in relatively small space; that groups of social bees tend to be relatively more quiet when in vials than are isolated individuals, while the opposite relation holds with bees belonging to solitary species. Some such differences in behavior are to be expected and further critical experiments may demonstrate that such behavior differences are mirrored in the toleration of adverse experimental conditions by grouped and isolated bees, as suggested in the previous section. The data at hand have allowed us to recognize the problem and to indicate the method whereby its solution may be attempted.

D. Experiments With Groups and Isolated Bees Indicate That Survival Results Given in Section IV C Have Been Affected by Including Social, Semi-social and Non-social Bees in the Same Mass of Experimental Data

Toleration experiments with groups and isolated social and semi-social bees of the families *Apidae*, *Bremidae*, and *Halictidae*, and with the non-social bees of the family *Euceridae*, indicated a shortening of the expected life-period of any isolated bee of the first three families, while less varied experiments were inconclusive with those bees of the *Euceridae*. If the im-

perfect results at hand have value, it must therefore be noted that survival data obtained by the study of isolated bees, as reported in Section IV, have been thrown open to question by having included social, semi-social, and non-social bees in the same tables for comparisons. However, these data have been rendered incorrect for comparison only in so far as it can be shown that, for example, solitary species of Euceridae have been included as more or less than half of the cases where "dry" habitat bees are compared as to survival under dry conditions with "moist" habitat bees, while social species of *Bremidae*, which would count isolation from their fellows as an additional lethal factor, form less or more than half the cases where "moist" habitat bees are compared as to survival under dry conditions with "dry" adapted bees. If half the cases of "dry" adapted bees are social or semi-social with the other half non-social, while the same holds true for the "moist" adapted contrasted cases, then the data are altered on both sides and no harm is done.

Referring to Tables IX and XI, which give the data concerning experiments with isolated bees, described in Section IV, we observe that under conditions of high temperature and low humidity the following numbers of bee species and sexes were used, and these bees were characteristically found in the types of environment given (see Table XXII).

Inspection of the summary of the kinds of bees used (Table XXII) in the experiments with isolated individuals, reveals the fact that the majority

TABLE XXII—*Numbers of species and sexes of social-semi-social and of non-social bees found to frequent certain habitats and used in toleration experiments as isolated bees*

Bee Types	Experiments with Groups and Isolated Bees				Odd Experiments with Isolated Bees				Total
	Habitat			Total	Habitat			Total	
	Moist	General	Dry		Moist	General	Dry		
Social or Semi-social	6	13	4	23	5	2	3	10	33
Non-social	3	5	11	19	2	2	15	19	38
Total	9	18	15	42	7	4	18	29	71

of the social or semi-social bees used were considered as being either "general" or "moist" in their habitat distribution, while the majority of non-social bees used come under a "dry" category. These points not only show that the data with isolated bees of Section IV C have been affected if later experiments should prove that non-social bees tend to live longer when isolated, while social and semi-social bees tend to have their life period shortened when isolated, but also raise the question whether social and semi-social bees may not be more widespread in distribution (throughout the year as well as throughout various habitats), and thus in reality be the more vigorous and resistant of the bees.

The three families mentioned, *Apidae*, *Bremidae*, and *Halictidae*, including the social and semi-social bees, do fly, as suggested above, from early in the spring until late in the fall. Not all species and not all sexes will be on the wing, but the majority of the species can be collected as worker or female as long as flowers are in bloom and the weather is good. The non-socials, on the contrary, have definite flight-periods which are mostly short. Seasonal variations in humidity and temperature thus present opportunity for other possible correlations with the physiology of these bee species.

The social and semi-social bees must spend a considerable portion of their time in the nest with other bees, where the humidity must be assumed to be high. From this region of safety and comfort, the bees wing out, periodically, into all environments or habitats, collecting and working as they will, losing water in the dry regions, but able to return to the nest long before the water loss becomes serious or lethal. Perhaps, then, we can say that they are not only possibly more resistant, but are also in reality "moist" adapted bees, though their flower visits would place the majority of them as "general" in distribution, according to our classification as given in Table XXII and earlier tables.

Now comparing the non-social bees, we find them emerging from their cells when the pupal stage is over, and flying to their flowers or to their plant communities, but making no effort to return to a communal nest having constant temperature and humidity, even though they may all build nests in the same general locality. If adapted to dry conditions, they visit dry habitats mainly, and even may build their nests in these regions. (It is recognized, of course, that in dry regions any bee will tunnel through sand or clay or wood to reach some moisture for the nest, if this is possible.) If adapted to moist regions, the bees will tend to remain in this type of environment. In the case of oligoleges we have reasons for assuming that they nest near their flower-food sources.

The general suggestion of social and semi-social bee adaptation to moisture depends upon the proof of the high humidity of the nest. Most persons will doubtless grant the assumption for *Apidae* and *Bremidae*. The survival data for *Apidae* exposed to high temperature and high humidity (Table XX) compared with survival at low humidity (Table XVI) will go a long way in the establishment of this premise. But few will be willing to concede that the majority of the *Halictidae*, with their tunnels and branches, have a nest that is maintained at high humidity. In this connection, let me suggest that the female Halictid whom every entomologist has seen at the common-gallery entrance with head fitting snugly in the passage and facing outward is not there only to guard against intruders, but may also be serving instinctively or otherwise as a door to keep the moisture inside, on warm dry days. If she were a sentinel only, it is inconceivable that she should allow the parasitic Sphecodes to enter and lay her eggs.

The data obtained from experiments carried on with groups and isolated individuals probably have little effect toward altering any decisions concerning the correlation between bee-survival and habitat-conditions. It was stated in Section IV that certain bees apparently were adapted and others were not. It was pointed out that *Halictidae* apparently showed no correlation. If they are mesic or "moist," as assumed because most of them are semi-social, this lack of correlation is explained. The apparent correlation, of *Bremidae* survival with environment, required omitting the data available from *Bremus americanorum* females and may have been due to chance. It will be noted that all of the bees involved are given a "general" distribution and only *Bremus separatus* is shown as having emphasis on prairie visits.

VI. CONCLUSION

During two seasons it has been possible to collect specimens of at least one sex of over half of the species of bees to be found within a radius of seventy-five miles of Chicago. This has been accomplished with little collecting in the dunes regions and with major emphasis placed on morainic oak and semi-climax, flood-plain, and prairie. Weeds and ruderals, old fields and orchards, have not been disdained. It will require several additional seasons to cover all communities at all necessary times of the year.

With these species, given mainly according to the terminology of Robertson, it has been possible to cite either the original record of description of the bee, or else a better description has been added, or at least a key record which will remove the bee from the category of being only a name.

Comparison of the bee-flower relationships, given by Robertson (1928), with the flower-community data of Fuller (1925) and Pepoon (1927) (Appendix B) and local bee collection data, indicates that it is fair to assume that the bees and flowers known to have definite relationships in the Carlinville area can be expected to maintain the same general relationships if both the bee and the flower occur in the Chicago area. From these data, it is even possible to predict bee visitors and communities visited in the dunes series. The extent to which this is only a prediction is quite evident to the reader and confirmatory or corrective evidence is much to be desired.

From Robertson's data, it has been possible to indicate local plant communities which certain bee species will be expected to visit more frequently than other communities. From these data, it has been possible to assign certain environmental characteristics as being the ones most frequented by given bees. Even without collecting in the dunes regions, Robertson's data offer interesting correlations of species peaks of certain families in certain communities of the dunes sere. Tables III and IV should be compared with Park (1930). Study of these tables indicates that the more flowering plants in a given community, the fewer bees will visit each plant. Predictions from

Robertson's data range from 17.3 bees per flower in the tamarack stage of the peat bog community, to 1.85 bees per flower in the flood-plain community.

Bees have been classified according to the physical characteristics of the communities they visit most frequently. Certain bees have been characterized as "general,"—that is, visiting all communities with about equal frequency; "dry,"—that is, "preferring" or visiting the communities where humidity is lower or rate of evaporation is higher; and so on.

Large numbers of the bees have been brought back alive to the laboratory and tested under controlled conditions of constant humidity and temperature. These experiments have shown that high temperature (41°C.) exerted a decidedly lethal effect upon all species of bees tested. They also showed that low relative humidity (25% or lower) exerted a less noticeable lethal effect, more variable from species to species. Extremely high relative humidity (over 85%) was also shown to exert a lethal effect, though fewer experiments of this nature were made than with the other conditions.

These experiments indicated that there was a general correlation between rapidity of lethal effect of low humidity and smallness of bee size. But they also showed that, in cases of low humidity and high temperature, there was a definite correlation (when all the kinds of bees used were weighted for size and averaged) between survival time and character of habitat most frequented by the bees under consideration. Bees most characteristically taken in regions of high humidity and low evaporation rate were shown to die sooner, under conditions of high temperature and low humidity, than did bees found to frequent a more dry region of low relative humidity. Bees that were considered as "general" or visiting all types of communities indiscriminately, in at least one series of data, indicated longer survival than either "moist" or "dry" adapted bees. It may be concluded that these "general" bees would prove most hardy, if averaged under all conditions of lethal character and compared with "moist" or "dry" adapted bees tested under the same sets of conditions. The question of supposedly "general" social bees being in reality "moist" is discussed later.

Experiments are needed to determine whether the so-called "oligoleges" of Robertson occurring in certain communities are apparently adapted to the environmental conditions, or seek the host flower and are unaffected by the physical factors. It is probable that the bees might be adapted to both the flowers and the physical characters, at least in some instances. If this were true, either adaptation might have preceded the other.

From the data, the conclusion must be reached that there are certain species of bees characteristic of certain plant communities. Other bees most certainly must be considered "general," in flower-visit distribution at least. Then any lists of the animals of a plant community should most certainly include numerous species of bees, some of them as casual visitors, others as visitors restricted either entirely or in part.

Comparison of survival of groups and isolated bees, of these various species of bees, indicates a possible difference in survival, between the social or semi-social bees and the non-social or solitary bees. The social or semi-social bee groups are shown to outlive the isolated bees. Data from the non-social bees are inconclusive, though suggestive, and further experimentation is necessary.

Consideration of these facts, in the light of the experiments with isolated bees only, suggests the possibility that social or semi-social bees are really adapted to moist conditions of high relative humidity and are moist, dry, or general in their flower-community visits due only to flower preference or abundance. This explanation has the advantage of solving the question of the longer group-survival by ascribing it to communal "effort" to block air flow, as well as to "soothing" effects of other members of the group in cutting down activity and metabolism and permitting an effective massing, thus invoking the surface-mass ratio.

Solitary bees, no matter how adapted to dry environments, may be adversely stimulated to activity by the presence of other bees.

The habit of the *Halictidae*, of blocking nest-gallery openings with their heads, would seem to give added evidence for the assumption that the majority of the species of this family of semi-social bees maintain high humidity in the nest.

Furthermore, this assumption, that there is adaptation to "moist" conditions among the *Halictidae*, would seem to explain the lack of correlation between apparent environmental adaptations and actual survival in experiments with the *Halictidae* (see particularly Tables XIII and XIV).

Further experiments should be undertaken. Live bees should be taken without a net, should be transported at once to the laboratory, and experiments should be made without delay. These experiments should most certainly be made with additional species of supposedly non-social or solitary bees. Toleration experiments using groups and isolated specimens of these species may bring to light other bees developing social habits and may confirm or correct the suggestions along that line advanced in this work.

VII. SUMMARY

1. A complete check-list for the bees of any locality possessing habitats of the variety of those in the Chicago area would require a considerable number of years to complete. It has been possible by extensive collecting, however, to prepare in two seasons a representative list undoubtedly including certain data concerning over half of the species to be expected within a seventy-five mile radius of Chicago. One hundred and sixty-nine species have been identified.

2. The similarity of the floras and bee faunas of the Carlinville and Chi-

cago areas justifies making use of data accumulated by Robertson in the Carlinville area, which deal with relations between bees and flowers,—one of the closest of plant-animal relations.

3. Certain comparisons have been made of relations between flowers and bees predicted from Robertson's records with records accumulated in the Chicago area and they further justify using the Southern Illinois data.

4. It seems to be true that, though there is a frequent "preference" for some community or community type, bees are to be thought of as "following" the flowers and as being probably secondarily adapted to the communities which they are thus led to frequent. Only occasionally is it possible to indicate a bee as a visitor to only two or three communities. Yet it is quite feasible to present lists of bees to be expected in the various communities at the proper seasons if the collector makes sure to visit the community at all times of the blooming season.

5. Certain families of bees are shown to be more characteristic of a given community than of another. *Apidae, Bremidae (Bombidae),* and *Halictidae* are the most ubiquitous.

6. It has been possible to bring live bees into the laboratory and test their survival under varying conditions of temperature and humidity, in order to examine whether there is a correlation between survival and type of community most frequented. There is some indication that such correlation exists among certain bees. It was most definitely shown that bees visiting all kinds of communities are in general more hardy than bees restricted to dry or moist conditions. The smaller the bee, the less possibility of detecting physiological adaptation to moisture or dryness, if such adaptation exists.

7. Checking groups and isolated individuals of bees under experimental conditions indicated a general adaptation permitting social or semi-social bee groups to live longer than isolated individuals. No conclusive data have as yet been obtained for the non-social bees.

8. The data suggest a general adaptation of semi-social and social bees to moist conditions, their nesting habits permitting them to have such an adaptation and yet visit all types of communities. Non-social bees appear to be adapted to either moist or dry conditions, according to the communities in which they nest and which they frequent while collecting pollen and other substances.

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APPENDIX A

ROBERTSON'S REVISED LIST OF OLIGOLECTIC BEES

This list of oligoleges and their pollen flowers is modified from "Ecology," VII, 1926, originally incorrectly printed in "Ecology," VI, 1925. Of the 83 oligoleges in this list, the writer has collected specimens of 37 species, designated in each case by a single "c" following the species name. Of the 37 taken in the Chicago region, 19 species have been observed collecting pollen on the designated host or on one of the host group and are designated by "cc." There is some question concerning the validity of Robertson's *Melissodes boltoniae*. If it is a true species, the writer has specimens.

Andrena arabis	c	Cruciferae
erythrogastra		Salix
illinoensis		Salix
macoupinensis		Salix
nigrae		Salix
nothoscordi		Nothoscordum striatum
nubecula	c	Astereae
salicacea		Salix
salicis		Salix
salictaria	cc	Salix
Iomelissa violae		Viola
Opandrena ziziae	c	Umbelliferae, zizioid
Parandrena andrenoides	cc	Salix
Pterandrena aliciae	cc	Heliantheae
asteris		Astereae
helianthi	cc	Astereae, Heliantheae
krigiana	c	Krigia amplexicaulis
pulchella	c	Heliantheae
rudbeckiae	cc	Heliantheae
solidaginis	cc	Astereae
Ptilandrena erigeniae	cc	Claytonia virginica
g. maculati	c	Geranium maculatum
polemonii	c	Polemonium reptans
Trachandrena mariae	cc	Salix
spiraeana		Aruncus sylvester
Colletes aestivalis		Heuchera hispida
albescens		Petalostemum purpureum
americanus	cc	Astereae, Heliantheae
armatus	cc	Asterae
brevicornis		Specularia perfoliata
compactus	cc	Astereae, Heliantheae, Helenieae

latitarsis	c	Physalis
robertsonii		Petalostemum purpureum
willistoni	c	Physalis
Halictoides marginatus	cc	Helianthus
Chloralictus nymphaearum		Nymphaeaceae
Macropis steironematis		Steironema
Anthemurgus passiflorae		Passiflora lutea
Calliopsis coloradensis		Heliantheae, Astereae
Perdita octomaculata		Astereae, Heliantheae
Perditella boltoniae		Boltonia asteroides
Pseudopanurgus albitarsis	cc	Heliantheae
asteris		Astereae, Heliantheae
compositarum	c	Astereae
labrosiformis		Heliantheae
labrosus	c	Heliantheae
rudbeckiae		Heliantheae
rugosus		Heliantheae
solidaginis		Astereae, Heliantheae
Verbenapis verbenae		Verbena
Zaperdita maura		Physalis
Amegilla walshii	c	Cassia chamaecrista
Emphor bombiformis		Hibiscus
Melitoma taurea		Ipomoea
Anthedon compta		Oenothera biennis
Cemolobus ipomoeae	(ol.?)	Ipomoea pandurata
Epimelissodes atripes		Cassia chamaecrista
illinoensis		Heliantheae
Melissodes agilis	cc	Astereae, Heliantheae
asteris		Astereae
autumnalis		Astereae, Heliantheae
boltoniae	c(?)	Astereae, Heliantheae, Helenieae, Cichorieae
cnici	cc	Cirsium
coloradensis	cc	Heliantheae, Cynarieae
coreopsis		Coreopsis palmata
simillima	cc	Astereae, Helenieae
trinodis	cc	Astereae, Heliantheae, Helenieae
vernoniae		Vernonia fasciculata
vernoniana	cc	Vernonia fasciculata
Peponapis pruinosa		Cucurbita pepo
Tetralonia robertsonii		Papilionaceae
Xenoglossa strenua		Cucurbita pepo
Anthidium psoraleae		Papilionaceae
Ashmeadiella bucconis		Astereae, Heliantheae
Gnathosmia georgica		Astereae, Heliantheae, Cichorieae
Megachile generosa	c	Leguminosae
sexdentata		Heliantheae, Astereae
strophostylis		Strophostyles helvola
Oligotropus campanulae	c	Campanula americana
Sarogaster georgica		Papilionaceae

Sayapis pollicaris .....Heliantheae
pugnata .....cc....Heliantheae, Cynarieae
sayi .....c....Heliantheae, Cynarieae, Eupatorieae

APPENDIX B

PLANT "ASSOCIATIONS" OR COMMUNITIES OF THE CHICAGO REGION

Section A. Fuller's Associations.[1]—The roman numerals, or roman numerals followed by arabic numerals represent associations designated in Fuller (1925). The first column of arabic figures is used to designate the same associations but is used with flowers which do not appear in Fuller's list, but have either been stated by him to be found in the association designated, or have been placed there by reference to the description of the habitat of the flower, as given by Pepoon (1927).

I. The Sand Dune and Upland Associations

1. I-1 The Beach Association
2. I-2 The Fore-dune Associations
3. I-3 The Cottonwood Association
4. I-4 The Pine Dune Association
5. I-5 The Black Oak Association
6. I-6 The Mesophytic Oak Forest Association
7. I-7 The Climax Mesophytic Forest
8. I-8 Sandy Swamp Associations

II. The Prairie Associations

9. II-1 Low Prairie
10. II-2 High Prairie

III. Aquatic Associations

11. III-1 Submerged Aquatics
12. III-2 Floating-leaved Aquatics
13. III-3 Emergent Aquatics
14. III-4 Reed Swamp Associations
15. III-5 Sedge Swamp Associations

IV. The Peat Bog Associations

16. IV-1 The Sedge Association
17. IV-2 The Xerophytic Shrub Association
18. IV-3 The Tamarack Association
19. IV-4 The Pine Birch Forest Association

20. V. The Rock Ravine Associations
21. VI. The River Cliff Associations
22. VII. The Flood-Plain Associations
23. VIII. The Lake Cliff Associations

[1] Here Fuller's terminology has been followed, despite the fact that more recent terminology might break the associations up into associes and other more specialized groups. Elsewhere in this work these associations have been referred to as communities.

Section B. Man-dominated and other communities.—These communities are made up from designations given verbally by Fuller and are applied only to plants from Robertson (1928), which are not listed in Fuller (1928) as being characteristic of natural communities in the Chicago region. These communities do not appear elsewhere in the data but are given as references for future collecting.

24. Hillsides
25. Dry grasslands
26. Moist grasslands
27. Sandy soil
28. Ditches
29. Thickets
30. Pioneer
31. Burned clearings
32. Open dry situations
33. Railroad embankments
34. Ruderal
35. Old fields, old pastures, waste places
36. Orchards and fields
37. Meadow weed
38. Forest weed
39. Garden weed
40. Dooryard, barnyard weed
41. Weed
42. Introduced
43. Cultivated
44. Escaped cultivation
45. Cosmopolitan
46. Parasite
47. Existence doubted, very rare, old record, etc.

DIE ERNÄHRUNGSÖKOLOGISCHEN BEZIEHUNGEN ZWISCHEN *ASIO OTUS OTUS* L. UND IHREN BEUTETIEREN, INSBESONDRE DEN MICROTUS-ARTEN

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DIE ERNÄHRUNGSÖKOLOGISCHEN BEZIEHUNGEN ZWISCHEN *ASIO OTUS OTUS* L. UND IHREN BEUTETIEREN, INSBESONDRE DEN MICROTUS-ARTEN

I. EINLEITUNG UND FRAGESTELLUNG

Die Beschaffenheit einer nicht gestörten Biozönose bleibt während längerer Zeit annähernd dieselbe, das heisst dass dieselben Arten während längerer Zeit in demselben zahlenmässigen Verhältnis nebeneinander leben. Dieses ist umsomehr verwunderlich, weil wir ja sehen, dass Änderungen in der Anzahl der Individuen jeder Art in kurzer Zeit vor sich gehen können. Diese kürzeren Bewegungen in der Beschaffenheit der Biozönosen, diese Schwankungen im ökologischen Netz, werden aber meistens schon bald wieder ausgeglichen, m.a.W. die Biozönose bewegt sich immer um ein gewisses Gleichgewicht herum, ein Gleichgewicht das aber immer nur annäherend und vorübergehend erreicht wird, und also in der Natur nicht besteht. "'The balance in Nature" does not exist and perhaps never has existed." (Elton, 16). Es sind zwei einander entgegengesetzte Kräfte, die sich hier gelten lassen: die Fortpflanzung der Tiere unter optimalen Verhältnissen, welche die Anzahl der Individuen steigert, auf der einen Seite; und *alle* Faktoren, die eine solche Vermehrung hemmen, auf der anderen Seite.

Einer dieser Faktoren ist die Ernährung, die eine hemmende Wirkung auf beide Tiergruppen, die Raubfeinde und die Beutetiere, ausüben kann. Unter diesem Gesichtspunkt lassen sich an unseren Eulen interessante Beobachtungen sammeln, weil sich die Nahrung verschiedener Eulenarten aus den in ihren Gewöllen vorhandenen Resten der Beutetiere verhältnismässig gut herausfinden lässt. Zumal *Tyto alba*, die Schleiereule, ist daher von mehreren Forschern schon eingehend studiert worden.

In der Absicht, unsere Kenntnisse von der Nahrung der Waldohreule zu erweitern, fingen mein Bruder L. Tinbergen und ich im Winter 1929-'30 an, gelegentlich die Gewölle dieser Eule zu sammeln. Als wir noch recht geringe Resultate hatten, erschienen die höchstinteressanten und mit grosser Ausdauer fortgeführten Untersuchungen Uttendörfer's und seiner Mitarbeiter (72). Allmählich lernten wir hierüber mehr Literatur kennen; diese befriedigte uns aber nicht ganz und das regte uns dazu an, die angefangenen Untersuchungen fortzusetzen, und einerseits durch weitere Problemstellung, andererseits durch etwas feinere Methoden unsere Einsicht in die wechselseitigen Beziehungen zwischen der Eule und ihren Beutetieren zu vertiefen.

Schon bald erwies sich auch hier, dass der Inhalt der Gewölle nicht nur in verschiedenen Gegenden ziemlich verschieden war, sondern auch in derselben Gegend mit der Zeit erheblich schwankte. Von diesem Augenblick an

tauchten die Fragen auf: inwieweit beeinflusst die Beschaffenheit des Nahrungsvorrates, d.h. die Zusammensetzung der Biozönose, die Speisezettel der Eule; welchen Einfluss übt die Eule auf das Leben seiner Beutetiere aus? Umgekehrt: welchen Einfluss haben die Änderungen in dem Nahrungsvorrat auf die weiteren Lebensvorgänge der Eulen? Und schliesslich: was sind die allgemeinen psychologischen Grundlagen für das Verhalten der Eulen in ernährungsökologischer Hinsicht?

Es sind dies alles sehr komplizierte Fragen, die in den verschiedenen diesbezüglichen Veröffentlichungen teilweise berührt werden, von deren Lösung wir aber noch weit entfernt sind. Es wird dem Leser denn auch auffallen, dass ich hier und da auf eine Frage näher eingegangen bin ohne mich dabei auf das nötige Tatsachenmaterial stützen zu können. Diese Gedankenausflüge sind aber in der Absicht gemacht worden manche offene Frage hervorzuheben. Ausserdem fiel mir bei der Durchsicht der Literatur auf, wie unabhängig voneinander die verschiedenen Untersucher arbeiteten. Zumal die Trennung der englischen und deutschen Untersuchungen ist auffällig; ich habe mich wo nötig bemüht Arbeiten aus diesen verschiedenen Kategorien im Lichte eines Problems zusammenzufügen.

Das Feldwerk, zumal das regelmässige Sammeln der Gewölle und das Aufsuchen verschiedener Überwinterungsstellen der Waldohreulen nahm ziemlich viel Zeit in Anspruch. Obwohl wir in der Regel unser Material selbst sammelten, haben wir doch manchmal, namentlich in altbewährten Waldohreulengebieten, Hilfe verschiedener Mitarbeiter nicht verschmäht; für diese tätige Hilfe sprechen wir den Herren J. Ebbinge Wubben, B. Koens, H. Naeser, J. ter Pelkwijk, M. G. Rutten, D. Tuynman und R. de Wit unseren besten Dank aus. Sehr zu Dank verpflichtet haben uns: Frl. D. Out, Herrn und Frau H. J. Van Houten-Van der Looy van der Leeuw, sowie die Herren K. J. Karseboom, J. Kikkert, J. Reuter und A. de Wijs, die uns in verschiedenen Teilen des Landes mit Waldohreulengebieten bekannt machten. Den Herren L. D. Brongersma (Leiden) und Dr. G. Barendrecht (Amsterdam) schulde ich Dank für einige Artbestimmungen.— Am Untersuchen der Gewölle nahmen mein Bruder L. Tinbergen und ich etwa gleichen Teil; die stetige Diskussion im Laufe der Arbeit ist deren Gründlichkeit zugute gekommen.

Bleibt noch einiges über die Verwertung der Literatur zu sagen. Wie es in der Ökologie und zumal in der ökologischen Ornithologie die Regel bildet, finden sich über unsere Frage zahlreiche kleinere Mitteilungen in den verschiedensten Büchern und Zeitschriften zerstreut. Diese Literatur auch nur annäherend zu verwerten schien mir nicht gut möglich. Für mancherlei Hinweise auf mehrere Quellen bin ich den Herren Dr. Jan Verwey (Helder), Ludwig Schuster (Berlin) und O. Uttendörfer (Herrnhut) sehr zu Dank verpflichtet.

II. METHODEN

Wie bekannt werfen die Eulen regelmässig Gewölle aus, in denen die unverdauten Reste der Beutetiere fest zusammengeballt sind. Diese Reste sind Haare und Federn, Chitinteile und Knochen. Im Gegensatz zu den Raubvögeln verdauen Eulen die Knochen gar nicht sondern wir finden die feinsten Splitter in den Gewöllen zurück. Wir können also die Gewölle sehr gut zur Untersuchung der Nahrung heranziehen, ohne der Gefahr ausgesetzt zu sein, gewisse Beutetiere nicht in den Gewöllen zurückrufinden und sie somit zu vernachlässigen.

A. DAS SAMMELN DER GEWÖLLE UND DAS BESTIMMEN DES URHEBERS

Die Waldohreule jagt im Allgemeinen am Tage nicht, sondern sie zieht sich meistens in den Wald zurück um die tägliche Ruhepause zu verbringen. Sie bevorzugt hierzu dichte, nicht zu alte Koniferenbestände und hat hier meistens einige bevorzugten Ruhebäume. Unter diesen Ruhebäumen finden wir die Gewölle; hier sind sie regelmässig zu sammeln ohne dass die Eule hierdurch veranlasst wird umzusiedeln, was das Sammeln sehr erschweren würde.

Die Bestimmung des Urhebers der Gewölle ist in diesem Fall nicht schwierig. Bei regelmässiger Sammeltätigkeit lassen sich die Eulen auf ihren Ruhebäumen direkt beobachten. Es passiert einem gar nicht selten, dass die Eule ruhig an der Stelle bleibt, während man unter dem Ruhebaum herumläuft. In jedem unserer Sammelgebiete haben wir die Eulen in dieser Weise viele Male beobachten können.

In den Monaten Juli und August mausern die alten Waldohreulen; in den Monaten August und September die im Sommer erbrüteten Jungen. In dieser Zeit geben also die im Bestand insbesondre unter den Ruhebäumen herumliegenden Mauserfedern weitere zuverlässige Auskunft über den Urheber der Gewölle.

Wir wissen nicht, inwieweit wir bei solchen Ruhebäumen darauf schliessen dürfen, dass nicht auch gelegentlich Eulen anderer Arten sich hier aufhalten. Es ist gerade in der Zugzeit nicht unmöglich, dass Durchzügler während einiger Zeit in Waldohreulengebieten verbleiben, ohne dass wir sie direkt beobachten können. Zumal von den Sumpfohreulen wissen wir, dass sie sich gelegentlich an ähnlichen Stellen wie die Waldohreulen aufhalten, und das könnte uns dadurch irreführen dass ihre Gewölle von denen der Waldohreulen ziemlich schwierig zu unterscheiden sind. Wir müssen dieser Möglichkeit Rechnung tragen, können aber mit Recht behaupten, dass eventuelle hierdurch entstandene Fehlerquellen sehr klein und somit zu vernachlässignen sind.

Im Zusammenhang hiermit interessiert uns die Frage, inwieweit es unter den Eulen Territoriumbehauptung gibt. Es bildet unter den verschiedensten Vögeln die Regel, dass ein Brutpaar ein bestimmtes Gebiet als das seine behauptet und verteidigt (Howard, 32) und bei den Raubvögeln scheint dies ebenfalls vorzukommen. Wie aber die verschiedenen Eulen sich unter sich verhalten weiss ich nicht; ich kenne keine diesbezüglichen Angaben in der Literatur, und die wenigen Beobachtungen die ich selbst

sammelte sind noch zu fragmentarisch.—Sicher ist aber, dass die Waldohreulen sich ausserhalb der Brutzeit zu Trupps anschliessen. In unserer holländischen Dünengegend überwintern an vielen Stellen regelmässig solche Trupps, die meistens 5-15, manchmal für kurze Zeit bis zu 30 Stück zählen. Immer habe ich in diesen Gesellschaften nur Waldohreulen gesehen. Ich weise auf diese Dinge hin, weil genaue Kenntnisse dieser Umstände unsere Methodik verfeinern und daher unsere Schlussfolgerungen sicherer stellen könnten.

Auf eine interessante Tatsache sei hier noch aufmerksam gemacht: Es sind mehrere Fälle bekannt, wo Turmfalken und Waldohreulen ihre Nester in unmittelbarer Nähe voneinander, manchmal im selben Baum, hatten, nur einen oder zwei Meter voneinander entfernt. Dasselbe sieht man bei Turmfalken und bei Waldohreulen innerhalb der Art nie. Dieses ist deshalb eine höchst merkwürdige Tatsache, weil man aus dem Verhalten vieler territoriumbehauptenden Vögel den Eindruck gewinnt, dass eine der wichtigsten ökologischen Bedeutungen dieses Verhaltens ist, dass den Jungen hinreichend Nahrung versichert wird. Eine zweite ökologische Bedeutung ist die Versicherung einer günstigen Niststelle. Nun sind Turmfalke wie Waldohreule einander sehr ähnlich, sowohl was ihre Nahrung als was ihren Vorzug für alte Krähennester anbetrifft; sie sind also in verschiedener Hinsicht Konkurrenten; trotzdem dulden sie einander in nächster Nähe als Nistnachbar. Elton (15) hat darauf hingewiesen, dass es Tierarten gibt, die nur dadurch dasselbe Gebiet bewohnen können, dass die eine Art am Tage lebt, die andere eine nächtliche Lebensweise führt; möglicherweise handelt es sich hier um einen ähnlichen Fall.

Das Unterscheiden anderen Eulengewöllen gegenüber ist also in unserem Fall nicht schwer. Die Gewölle der Waldohreule und anderer Eulen sind von denen der Raubvögel zu unterscheiden durch die Beschaffenheit der Knochen. Während die Knochen der Beutetiere hier vollständig erhalten geblieben sind, sind sie bei den Raubvögeln immer stark angegriffen. Es kommt zwar vor, dass wir in Raubvogelgewöllen ganze unversehrte Knochen finden, dann sind aber immer auch noch unverdaute Weichteile vorhanden.

Wir gründen also die Bestimmung der Woldohreulengewölle a) den Gewöllen anderer Eulen gegenüber: auf direkte Beobachtung der Eulen selbst und auf das Vorhandensein zahlreicher Mauserfedern, im Zusammenhang mit der Tatsache, dass sehr bestimmte Ruhebäume während längerer Zeit benutzt werden; b) den Raubvogelgewöllen gegenüber ausserdem auf die charakteristische Beschaffenheit der Gewölle und der darin befindlichen Beutetierreste.

B. Das Bestimmen der Beutetiere und ihre quantitative Verwertung

Die Eule verschlingt fast immer ihre Beutetiere mit Haut und Haar. Vögel werden teilweise, manchmal auch sehr sorgfältig gerupft. Die Knochen gehen aber immer mit herunter. Dadurch dass auch die feinsten Knochensplitter von dem Magensaft der Eule nicht angegriffen werden, ist das Bestimmen der Säugetiere nicht schwierig. All unsere einheimischen Kleinsäuger sind am Ober- und Unterkiefer, manchmal an beiden, zu erkennen; man vergleiche hierüber die Arbeit von Miller (47).

Es ist schon öfters darauf hingewiesen worden, dass die Untersuchung der Gewölle der Eulen uns die besten Daten über die Verbreitung der Kleinsäuger geben kann. So ergeben unsere Gewöllfunde auf Texel, dass hier *Microtus ratticeps arenicola* De Selys Longch. die einzige Feldmaus ist. Unter ca 2000 Schädeln, welche wir untersuchen konnten, befand sich keine einzige andere *Microtus*-Art.

Die Vögel und die meisten anderen Tiere sind mit Hilfe von Vergleichsmaterial oft richtig zu bestimmen, die Knochen der Vögel sind aber gewöhnlich mehr oder weniger versplittert und daher lassen sich bezeichnende Stücke nicht immer finden. Bei der quantitativen Verwertung dieser Skelettfunde sind wir sehr vorsichtig gewesen. Bei den allgemein in den Gewöllen vorkommenden Tieren haben wir die Oberkiefer gezählt; bei seltener auftretenden Beutetieren ist manchmal derjenige Skeletteil, der in der grössten Zahl gefunden wurde, als Einheit angenommen. Diese Methode ist aber nur bei Einzelfunden erlaubt; bei periodischem Sammeln kann sie zu doppeltem Zählen führen. Die grösseren Beutetiere werden nämlich gewöhnlich nicht in einem Gewölle herausbefördert, sondern in zwei, drei oder gar vier Teilen. So fand ich z.B. einmal vier ganz frische Gewölle unter einem Ruhebaum. Jedes der vier Gewölle enthielt einen Teil einer Wanderratte; in dem ersten fand sich der Kopf, in den drei übrigen der Rest der Ratte. Dieses bildet für Wasserratten und Wanderratten die Regel.

Wir sind's nun zwar gewiss, dass wir alle in den Gewöllen befindlichen Beutetiere auffinden, nicht aber dass wir alle Gewölle finden. Über diese letzte Frage hat Guérin (26) in einer schönen Arbeit über die Schleiereule manches Interessante mitgeteilt. Auf Grund seiner äusserst sorgfältigen Beobachtungen kommt er zum Ergebnis, dass diese Eulen jede 24 Stunden regelmässig zwei Gewölle auswerfen, ein den am Abend gefangenen Beutetieren entsprechendes Nachtgewölle ("pelote nocturne") und ein den morgens früh gefangenen Beutetieren entsprechendes Taggewölle ("pelote diurne"). In der Regel werden nur die Taggewölle am "Ruheplatz" ausgeworfen, die Nachtgewölle lassen sich nicht an einer bestimmten Stelle auffinden, sondern liegen zerstreut herum. Ähnliche Feststellungen glaubt er auch an der Waldohreule gemacht zu haben. Wir würden daher nur einen Teil und zwar eine bestimmte Kategorie der Gewölle finden und daher nur einen Teil der von der Eule aufgenommenen Nahrung bestimmen können. Gegen diese Auffassung Guérin's ist nun der Einwand zu erheben, dass die von Uttendörfer aus seinen Gewöllfunden berechnete Menge der täglich benötigten Nahrung sehr gut mit den von Heinroth (28) an seinen gefangenen Eulen festgestellten Werten übereinstimmt, und bei Heinroth handelt es sich sicher um gesunde Vögel. Es ist aber sehr gut möglich, dass die Heinrothschen Eulen weniger Nahrung bedürfen als freilebende. Es wäre gewiss zufällig, aber daher nicht unmöglich, wenn diese beiden so verschiedenartigen Fehlerquellen dasselbe Resultat hätten!

Wie dem auch sei, die Feststellung Guérin's lässt wenigstens die Möglichkeit offen, dass wir auf den Ruheplätzen nur einen Teil der Gewölle finden. Auf absolute Werte lässt sich also vorläufig aus den Gewöllfunden nicht schliessen; der Inhalt der von Guérin untersuchten Tag- und Nachtgewölle der Schleiereule ist aber nicht essentiell verschieden; auf relative Werte können wir also allem Anschein nach aus den Gewöllfunden unter den Ruhebäumen wohl schliessen.

III. ALLGEMEINE ÜBERSICHT UNSERER ERGEBNISSE

Die Ergebnisse unserer Gewölluntersuchungen sind in der Tabelle 1 dargestellt. Es sei mir gestattet, mit einigen Worten hierauf einzugehen. Es fällt auf, dass *Microtus* das wichtigste Beutetier ist. *Microtus arvalis fulvus* (Geoffr.) ist in Holland bei weitem die allgemeinste Wühlmaus. Die überraschend grosse Menge *Microtus ratticeps arenicola* (De Sélys Longch.) stammt von der Watteninsel Texel. Dadurch dass Texel mit Feldmäusen und Waldmäusen dicht besiedelt ist, und sich an verschiedenen Stellen Kiefernstangenwäldchen befinden, überwintern hier verhältnismässig viele Waldohreulen.

Bezüglich der Mäuse muss betont werden, dass wir erst im Herbst 1931 anfingen, *Mus musculus* und *Micromys minutus* von *Apodemus sylvaticus* zu unterscheiden. Die Zahlen für beide müssen also höher sein; zwar viel höher sind sie wohl kaum, da erstens bei weitem die meisten echten Mäuse erst nach dieser Zeit zur Untersuchung gelangten und zweitens die Anzahl der *Mus musculus,* wo wir diese bestimmten, immer sehr niedrig war.

Die unter *Sorex* angeführten Spitzmäuse gehören vermutlich alle der Art *araneus* L. an. Im Winter 31-'32 fanden wir an verschiedenen Stellen sehr kleine Exemplare, die möglich der Art *minutus* L. angehören. Die Wasserspitzmäuse stammen alle von der Insel Texel, wo die Art häufig vorkommt. In texelschen Schleiereulengewöllen fanden wir auch immer *Neomys,* nie *Sorex; Sorex* scheint hier also nicht vorzukommen, *Crocidura* fanden wir dagegen einmal.

Kaninchen werden anscheinend, auch in Gegenden, wo sie sehr häufig vorkommen, nur ganz selten geschlagen. Meistens handelt es sich um junge Exemplare.

Die Fledermäuse können von der Eule im Flug ergriffen werden. Mein Freund Jan P. Strijbos teilt mir mit, dass er einmal eine Waldohreule einer fliegenden Fledermaus folgen sah, welche sie nach kurzer Zeit im Flug erhaschte.

Unter den Vögeln fällt der grosse Gehalt an Fringilliden auf. Erstens ist dieses dem Umstand zuzuschreiben, dass wir hauptsächlich im Winter sammelten, weil dann die Eulengesellschaften leicht aufzufinden sind. Zweitens wird die Eule wohl hauptsächlich gesellig schlafende Vögel erbeuten, und

hieraus wäre nicht nur der hohe Gehalt an Finkvögeln zu erklären, sondern auch die in verschiedenen Gebieten verhältnismässig hohe Anzahl der erbeuteten Drosseln. Wahrscheinlich handelt es sich hier hauptsächlich um Amseln, deren geselliges Nächtigen die Notizen Heyders (30) beschreiben. In einem unserer Waldohreulengebiete war ein solcher Amselschlafplatz ganz dicht neben und gar zwischen den Eulenruhebäumen.

Die Vögel lassen sich an den Schnäbeln oft gut unterscheiden, nur ein Unterschied zwischen Buchfink und Bergfink liess sich nicht herausfinden. Die Rubrik "Fink" enthält also beide Arten; dass die Waldohreule aber hauptsächlich die erste Art schlägt, geht klar aus den Rupfungen hervor. Die Rupfungen der Waldohreule sind deutlich von denen des Sperbers und denen des Merlins zu unterscheiden, denn die Waldohreule ist ausschliesslich Baumrupfer und daher liegen die Federn des gerupften Vogels ziemlich zerstreut herum. Die Rupfungen sind nur selten mitverwertet, nämlich nur, wenn das betreffende Beutetier in den Gewöllen nicht gefunden wurde. Zum Bestimmen des zahlenmässigen Verhältnisses des Buchfinken zum Berkfinken aber sind die Rupfungen gut zu gebrauchen.

IV. DIE ERGEBNISSE ANDERER FORSCHER

In der von mir durchgesehenen Literatur begegnete ich Angaben über deutsche, ungarische und dänische Waldohreulen.[1] Sie sind in den Tabellen 2, 3 und 4 zusammengestellt. Wie wir später sehen werden, sind die deutschen Beobachtungen, die durch ihren hohen Feldmäusegehalt auffallen, in der Hauptsache in Feldmäusejahren gemacht worden. Die dänischen Untersuchungen sind über eine Reihe von Jahren fortgesetzt worden und entsprechen der durchschnittlichen Nahrung wohl viel besser.

V. DIE SCHWANKUNGEN IN DER ZUSAMMENSTELLUNG DER NAHRUNG UND IHRE ABHÄNGIGKEIT VOM MILIEU

Vergleicht man die Nahrung der Waldohreulen zweier verschiedener Gebiete, so fallen manchmal grosse Unterschiede auf. Ich gebe einige Beispiele aus dem Winter 1931-'32.

Sehr viele Mäuse und Wühlmäuse, dagegen sehr wenige Vögel weisen die Speisezettel der texelschen Waldohreulen auf (Tabelle 5).

Einen auffällig hohen Waldmäuse-Prozentsatz trafen wir bei den Eulen von Ameland, einer anderen, hauptsächlich sandigen, Watteninsel (Tabelle 6).

Unweit von Haarlem fanden wir einen Trupp Waldohreulen, deren Gewölle sehr viele Spitzmäuse enthielten (Tabelle 7).

Unter Umständen können Waldohreulen auch hauptsächlich von Vögeln leben; ein Beispiel hierfür geben die Eulen, die sich in einem Garten in der

[1] Die Angaben von Collinge [Collinge, W. E.: The Food of some British Wild Birds. York (1924-'26)] konnte ich leider nicht berücksichtigen.

Stadt Rotterdam aufhielten (Tabelle 8). Diese Eulen schlugen fast ausschliesslich Hausspatzen.

Dass auch andere Vögel manchmal verhältnismässig viel geschlagen werden, zeigt uns Tabelle 9, welche die Nahrung einer auf der Insel Walcheren (Zeeland) in den Dünen überwinternden Waldohreulengesellschaft darstellt.

Es gibt noch eine zweite Variabilität in der Zusammenstellung der Nahrung und zwar eine im Laufe der Zeit. Die Speisezettel derselben Eulenindividuen können manchmal erheblichen Schwankungen unterliegen. Als Beispiel gebe ich die Speisezettel einer überwinternden Eulengesellschaft, die wir im Winter 1930-'31 und im Winter 1931-'32 auf ihre Nahrung untersuchten (Tabelle 10).

Diese Beispiele wären noch um viele andere zu vermehren. Wir sehen in solchen Fällen oft, wie ein bestimmtes Beutetier in der Nahrung einen wichtigen Platz einnimmt.

Die erste Frage, die man sich beim Durchsehen des Tatsachenmaterials stellt, ist folgende: Wie ist es zu erklären, dass die Nahrung der verschiedenen Eulen und die derselben Eulen im Laufe der Zeit sosehr verschieden sein kann? Diese Frage hat auch Uttendörfer sich gestellt. Anscheinend wissen wir hier selbstverständlich sofort Bescheid, denn es ist ja klar, dass eine Eule keine Spatzen schlägt in einem Land, wo keine Spatzen leben. Damit ist aber unsere Frage nicht beantwortet, denn die Eulen fressen nicht nur keine Spatzen in einem Land, wo es keine solchen gibt, sondern sie fressen bald viel, bald wenig Spatzen. Statt "Spatz" könnte man hier fast jedes andere Beutetier hinstellen. *Es fragt sich nun, ob diese Schwankungen in der Zusammenstellung der Nahrung immer durch übereinstimmende Schwankungen in der Umgebung der Eulen verursacht werden, oder ob hier auch andere Ursachen mit im Spiel sind.*

Bevor wir diese Frage weiter besprechen, seien einige Voraussetzungen gemacht. Wenn wir uns das Verhalten verschiedener Vogelarten ansehen, so erkennen wir hierin sehr viele arttypische Handlungen. So ist jeder Waldohreule z.B. eine arteigene Jagdweise angeboren, eine Jagdweise, die sie dazu zwingt, eben Mäuse und Vögel und keine Regenwürmer oder Fische zu fangen. Auch viele Unterschiede in der Nahrung verschiedener Eulen und Raubvögel werden von diesen Unterschieden in der Jagdweise bedingt, wobei die psychischen Fähigkeiten auch eine—und zwar hervorragende—Rolle spielen. Deshalb besteht manchmal ein deutlicher Vorzug für bestimmte Beutetiere und so ist es z.B. möglich, dass alle Sperber und vielleicht auch andere Raubvögel und Eulen einen arteigenen Vorzug für Vögel haben, aber oft Mäuse fangen, weil diese leichter zu haben sind.

So geht wahrscheinlich aus den Beobachtungen Hauchecorne's (*27*) hervor, dass der Maulwurf einen arteigenen Vorzug für Regenwürmer hat, worauf sein Jagd- und Fressverhalten besonders gut passt.

Der umgekehrte Fall: ein arteigener Abscheu gegen bestimmte Tiere, kommt zweifelsohne auch vor, und es sei hier nebenbei auf ein, ökologisch interessantes, Beispiel hingewiesen, das mir zufällig aus eigener Erfahrung bekannt ist. Ich war einmal in der Gelegenheit, während etwa zwei Wochen fast täglich einige Stunde eine kleine Anzahl jagender Fischreiher und einen fischenden Kormoran ganz aus der Nähe zu beobachten. Sie jagten in einem verhältnismässig kleinen Dünentümpel, der von Stichlingen, Garnelen und Kröten (*B. calamita* und *B. vulgaris*) bevölkert war. Es fiel mir hierbei auf, dass keiner der Vögel je eine Kröte erbeutete, obwohl eben diese Kröten sehr leicht zu ergreifen waren. Eine Untersuchung über die Nahrung des Fischreihers (67) zeigte, dass Kröten im Gegensatz zu Fröschen, Wasserratten und Fischen nicht erbeutet wurden (In den Jahren 1930 und 1931 (nicht veröffentlicht) bestimmten mein Bruder L. Tinbergen und ich 1675 Beutetiere, worunter 79 Frösche, aber keine einzige Kröte). Die Untersuchungen von Vasvari über die Ernährung der Rohrdommel (75) und des Purpurreihers (76) zeigen, dass auch diese Vögel keine Kröten fressen. In diesem Zusammenhang ist eine Angabe Liebe's (41) sehr interessant, worin mitgeteilt wird, dass Rohrdommeln verschiedene Kröten (*Bufo vulgaris, Bufo viridis* und *Bombinator igneus*) verweigerten, nachdem sie sie mit dem Schnabel angefasst hatten. Es scheint also, dass die erwachsenen Kröten tatsächlich regelmässig verschmäht werden.—Nach Hauchecorne (27) frisst auch der Maulwurf nie Kröten; verweigert diese, im Gegensatz zu Fröschen, auch in der Gefangenschaft. Das Verhalten eines Hundes Kröten gegenüber wird dem Leser bekannt sein.

Das Bestehen eines arteigenen Vorzugs für bestimmte Beutetiere hat aber für unsere Frage keine Bedeutung, weil es sich hier um die Schwankungen in der Nahrung einer und derselben Art handelt. Ganz unabhängig hiervon und für uns von grosser Bedeutung ist die Frage ob es einen individuellen Vorzug gibt.

Schauen wir uns jetzt Uttendörfer's Beobachtungen und Schlussfolgerungen an. Uttendörfer redet von "Spezialisten," wenn er es mit den Speisezetteln eines Vogels zu tun hat, in denen das auffällig häufige Vorkommen eines bestimmten Beutetieres nicht mit einer ähnlichen Häufigkeit in der Umgebung des Raubvogels übereinstimmt. Uttendörfer glaubt also für diese Fälle einen individuellen Vorzug verantwortlich stellen zu müssen. Zum besseren Verständnis seien einige Beispiele aus seinen Studien zitiert, woraus hervorgeht, dass er bald wohl, bald auch nicht auf individuellen Vorzug schliessen zu müssen glaubt.

Die reichhaltigsten Ergebnisse erzielte er beim Sperber (*Accipiter nisus*), dessen Beutetiere bekanntlich aus den hinterlassenen Rupfungen gut bestimmt werden können. Uttendörfer untersuchte in dieser Weise die Speisezettel von 180 Sperberbruten (bis 1930, später kamen noch viele hinzu); zwischen den einzelnen Sperberpaaren gab es erhebliche Unterschiede, die Uttendörfer in verschiedener Weise deutet, wie es die nachfolgenden Zitaten zeigen (72).

Seite 24 sagt er: "Ein äusserst bezeichnendes Abbild der Vogelwelt seines Wohnsitzes, des Parks mit seinen alten Eichen . . . ist die Beute des Muskauer Sperbers von 1920."

Zu den Beobachtungen Richard's (51) bemerkt Uttendörfer (S. 26): "Zu diesen klassischen Beobachtungen ist zu bemerken, dass offenbar auch ausgesprochenes Spezialistentum und zwar in Bevorzugung der Alpenbraunelle vorlieght, während der in solchem Terrain doch wohl häufigere Wasserpieper viel seltener gebracht wurde."

Am klarsten gehen Uttendörfer's Anschauungen aus seinen Bemerkungen auf Seite 27 hervor: "Zusammenfassend ist auf Grund dieser Speisezettel von Sperberhorsten zu sagen, dass sich die einzelnen Sperberpaare zwar nie völlig auf wenige Vogelarten beschränken, aber doch häufig ihre bevorzugten Jagdgebiete haben. Der eine jagt besonders im Wald, der andere auf Feld und Wiese, ein dritter im Dorf, andere endlich sind Mischtypen. Ja es zeigt sich deutlich, dass häufig eine bestimmte Vogelart, an die sich der Räuber offenbar gewöhnt hat, von einzelnen Sperbern einseitig bevorzugt wird, während sich andere Sperberpaare um dieselbe Art wenigstens während der Brutzeit gar nicht kümmern. So schwanken die Haussperling- und Feldlerchenrupfungen an unseren Horsten von je 42 und 40 bis 0, die von Dorngrasmücke und Kohlmeise von 37 und 27 bis 0, und bei Rauchschwalben hat es eine Sperberbrut gar auf 57 gebracht; andere Beispiele gehen aus den oben mitgeteilten Angaben über die einzelnen Bruten hervor. Dass dabei auch die Bestandsschwankungen der einzelnen Vogelarten in den verschiedenen Jahren mit einwirken, ist selbstverständlich. Dass daneben aber auch die Gewohnheiten der einzelnen Sperber eine ausgezeichnete Rolle spielen, dürfte aufgezeigt sein. Auch ergeben sich beachtenswerte Züge, wenn man den Horst in möglichst kurzen Zwischenräumen kontrolliert. Da findet man einerseits, dass diejenigen Arten, die gerade in halbflüggem Zustand, also möglichst bequem, zur Verfügung stehen, für eine kurze Zeit bevorzugt werden und dann manchmal gar nicht wieder vorkommen. Vor allem aber werden nicht wenige Sperberpaare, wenn die Brut die meiste Nahrung braucht, aus Wald- zu Dorfssperbern, sei es, dass der Wald nicht mehr genug Beute liefert, sodass also auch die Dorfspatzen herhalten müssen, sei es, weil sich dann auch das ♀ an der Jagd beteiligt, das vielleicht mehr an das Dorf gewöhnt ist als das ♂."

Soweit vom Sperber. Weiter interessieren uns die Waldohreulenbefunde Uttendörfer's. Seite 115 schreibt er: "Diese 20 Gewölle enthielten 19 Mus agrarius, 2 *Arvicola glarcola,* 5 *Sorex vulgaris,* 2 junge Hasen und 3 *Geotrupes,* zusammen 31 Tiere. Dieser Befund war insofern anormal, als die Feldmaus völlig fehlte und durch die Brandmaus ersetzt wurde, die offenbar damals eine Zeit starker Vermehrung hatte."

Seite 120: ". . . Geyr . . . hat die Gewölle von zwei Waldohreulen gesammelt, deren Schlafbäume 100 M. voneinander entfernt waren. In denen der einen fand sich keine Feder, bei der andern 16% Vögel. Es gibt also auch bei der Waldohreule Spezialisten."

Diese Zitaten genügen um zu zeigen, dass Uttendörfer für die Schwankungen in der Zusammenstellung der Nahrung verschiedene Ursachen annimmt. Manchmal sind die Speisezettel von dem in der Umgebung vorhandenen Vorrat von Beutetieren bedingt, manchmal aber hebt Uttendörfer hervor, dass der Spezialist auch in geringer Anzahl vorhandene Tiere in grösserer Menge zu erbeuten weiss, und doch—und hier ist die Inkonsequenz—schliesst er z.B. bei der Waldohreule aus einem, einen sehr hohen Prozentsatz an Brandmäusen ergebenden Fund auf eine Kalamität dieser Maus, und aus dem Unterschied in der Nahrung zweier verschiedener Eulenindividuen—die möglich verschiedene Jagdreviere haben !—auf einen Spezialisten.

Es sei hier ausdrücklich betont, dass dieses den Wert der schönen Arbeit Uttendörfer's und seiner Mitarbeiter nicht im geringsten Masse verringert. Nur ihre Studien können die Basis für weitere Untersuchungen bilden; gerade die Tatsache, wie oft diese Studien zitiert werden müssen, beweist dies. Das Thema ist aber keineswegs abgeschlossen.

Dass man nicht sofort auf individuellen Vorzug schliessen darf, wenn ein bestimmtes Beutetier mehr erbeutet wird als ein anderes, obwohl das zahlenmässige Verhältnis in der Umgebung umgekehrt ist (wie es das oben zitierte Beispiel mit den Alpenbraunellen und den Wasserpiepern Richard's zeigt) ist sofort klar, wenn man sich vor Augen hält, dass der Raubvogel es immer mit dem *erreichbaren* Nahrungsvorrat zu tun hat, das heisst, dass nicht nur die häufigst vorkommenden Tiere am meisten erbeutet werden, sondern auch die Tiere, die am besten zu der Jagdweise des Raubvogels passen. Aus der Tatsache, dass unsere Waldohreulen 224 Wanderratten und 9 Kaninchen erbeutet haben, wird niemand schliessen, dass in unseren Dünen 24 mal so viel Wanderratten als Kaninchen leben. Genau so ist es möglich, dass die Alpenbraunelle durch ihr Verhalten in manchen Gegenden sehr gut zu der Jagdweise des Sperbers passt und daher mehr als der Wasserpieper geschlagen wird.

An einer anderen Stelle bringt Uttendörfer denn auch eine Beobachtung, die vermutlich in dieser Weise zu deuten ist. Er findet bei einem Sperberpaar im Frühsommer verhältnismässig viele Grasmücken und erklärt dies durch die wohl richtig Annahme, dass sie während ihres "Balzfluges" eine leichte Beute für den Sperber sind.

Wir gehen also von der Voraussetzung aus, dass die Eule sich durch seine arttypischen, angeborenen Jagdorgane und Jagdverhalten eine Nahrungsumwelt schafft, die anders gestaltet sein wird als die Umwelt, die wir auf den ersten Blick um die Eule glauben sehen zu müssen. Deshalb wäre es auch kaum zu erwarten, dass die Nahrung der Eule die Verhältnisse, die wir in ihrer Umgebung sehen, quantitativ genau reflektierte.

Sehen wir uns jetzt die Tatsachen nochmals genauer an.

Wir können uns die verschiedenen Schwankungen und Unterschiede also in zwei Weisen enstanden denken: (1) durch individuellen Vorzug, (2) durch das Prinzip: "nimm was du kriegen kannst." Wie wir später sehen werden, ist im 2. Fall noch eine Komplikation dadurch möglich, dass (3) eine Gewohnheitsbildung an bestimmte Reviere mit ins Spiel kommen kann.

Es ist klar, wie wir zwischen der ersten Möglichkeit einerseits und der 2. und 3. Möglichkeit andererseits entscheiden können. Es gilt, bei jedem einzelnen Fall die Beziehungen der Nahrung zum Milieu zu untersuchen; finden wir immer eine Übereinstimmung zwischen den Abweichungen in beiden, so ist die 1. Möglichkeit ausgeschlossen, wenigstens nicht erwiesen. Finden wir in *allen* untersuchten Fällen diese Übereinstimmung, so wird die 1. Möglichkeit sehr unwahrscheinlich.

Um das Bestehen einer solchen Übereinstimmung in jedem einzelnen Fall mit Grund behaupten zu können, muss man annäherend die Zusammenstellung des Nahrungsvorrats kennen, das heisst erstens: man muss Bestandsaufnahmen machen und zweitens: man muss das Jagdverhalten des betreffenden Raubvogels einigermassen kennen und wissen welche Tiere unter den betreffenden Bedingungen als Beutetiere in Betracht kommen.

Was die Bestandsaufnahmen betrifft, so stehen wir hier vor keiner leichten Aufgabe. Wie Schuster (60) mit Recht betont, ist es sehr schwierig, die absoluten Zahlen der ein bestimmtes Gebiet bewohnenden Vogelindividuen jeder Art zu bestimmen. Viel schwieriger wird es, wenn wir auch noch die absoluten Zahlen der Klinsäuger ermitteln und mit denen der Vögel vergleichen wollen.

Es ist nun aber für unsern Zweck nicht erforderlich, dass wir absolute Zahlen wissen; wir brauchen bloss vergleichbare Zahlen, und hier sind Bestandsaufnahmen, wenn sie auch noch so mangelhaft sind, sehr von Nutzen, bloss mit dieser Voraussetzung, dass sie immer in derselben Weise vorgenommen werden. Ausserdem kann es einen erheblichen Unterschied machen, wenn zwei verschiedene Beobachter unabhängig nach derselben Methode zählen; in solchen Fällen sind grobe Fehler möglich. Man vergleiche hierüber auch Heyder (30) und zumal Herold (29).

Genaue Bestandsaufnahmen erfordern viel Zeit; es war uns daher nicht möglich, immer Nahrung und Milieu zu vergleichen. Eine kleine Anzahl unserer Beobachtungen gestattet aber einen Vergleich.

Wenden wir uns jetzt einer genaueren Betrachtung der Beobachtungen zu. In verschiedener Weise machten wir vergleichende Beobachtungen.

A. Wenn wir in einem bestimmten, mit einer Art der Beutetiere reich besiedelten Gebiet Waldohreulen trafen, untersuchten wir, ob die Häufigkeit dieser Art in der Eulennahrung in derselben Weise bemerkbar war und umgekehrt. Manchmal liessen sich solche Beobachtungen mit ziemlicher Genauigkeit machen.

B. In manchen Fällen war es uns möglich, in einem solchen Gebiet auch die Nahrung einer anderen Eulenart oder eines Raubvogels zu untersuchen. In diesen Fällen war es also möglich, die Nahrung zweier verschiedener, in verschiedener Weise jagender, Räuber zu vergleichen. Eine Übereinstimmung zwischen beiden Funden verringert die Möglichkeit, es mit zufälligen Übereinstimmungen zu tun zu haben.

C. Einige Male konnten wir im Jagdgebiet der Waldohreulen auffällige Schwankungen in der Individuenzahl eines Beutetieres wahrnehmen. Jedesmal wurden die Eulen daraufhin geprüft, ob sich auch in ihrer Nahrung dieselben Schwankungen bemerkbar machten.

D. Wenn es möglich war, auch jetzt die Nahrung der Eulen mit der Nahrung irgend eines anderen Räubers zu vergleichen, so wurde auch letztere auf dieselben Schwankungen untersucht.

A. Die Speisezettel der Eulen verschiedener Gebiete

1. Die Watteninsel Ameland besteht zum weitgrössten Teil aus Sanddünen; an der Wattenseite liegen sandige Wiesen, und fettere Wiesen oder Äcker lassen sich kaum finden. Es wird dem Leser klar sein, dass hier für Feldmäuse ungünstige Lebensbedingungen herrschen, und dass das ganze Gebiet fast ausschliesslich von Waldmäusen bewohnt wird. Hiermit stimmt die Nahrung der überwinternden Waldohreulen überein; in der Tabelle 6 ist diese dargestellt; die Feldmaus fehlt fast und die Waldmaus ist das wichtigste Beutetier.

2. Unsere Watteninseln, sogar die berühmte Vogelinsel Texel, zeichnen sich im Winterhalbjahr durch Armut an Singvögeln aus. Ausserdem sind die texelschen Dünen und Wiesen äusserst dicht mit Waldmäusen resp. Feldmäusen bevölkert. Die Speisezettel der texelschen Wintereulen gab ich schon in Tabelle 5, sie zeigen Armut an Vögeln, Überfluss an Feldmäusen.

3. Wo das Dünengelände feucht und bewaldet ist, kommen verhältnismässig viele Spitzmäuse vor. Das Landgut "Vogelenzang" bei Haarlem wird vom Polder aus künstlich bewässert und ist hierdurch ein günstiges Spitzmäusegebiet. Die Nahrung der sich hier aufhaltenden Eulen (Tabelle 7) zeigt denn auch einen ausserordentlich hohen *Sorex*-gehalt.

4. Einige Eulen auf Walcheren hielten sich in der Nähe des Dorfes auf, wo viele Hausmäuse erwartet werden müssen. Der Gehalt an Hausmäusen war hier auffallend hoch (Tabelle 9).

5. Eine Waldohreulenbrut in einem Kiefernwald unweit des Zuiderseestädtchens Harderwijk konnte ich im Sommer 1931 kontrollieren. Die alte(n) Eule(n) jagte(n) über dem feuchten, mehrere K.M. breiten Küstenstreifen, der mit Maulwürfen reich besiedelt war. Die hier untersuchten Waldohreulen haben die einzigen fünf Maulwürfe gefressen die wir für holländische Waldohreulen nachweisen konnten (Tabelle 11). Diese Ergebnisse habe ich an anderer Stelle schon mitgeteilt (68); siehe auch weiter unten.

6. Wie ich schon S. 509-'10 mitteilte, haben sich im Winter 1931-'32 einige Waldohreulen in Rotterdam aufgehalten, in der Nähe des Parks und des "Land von Hoboken," einer ziemlich grossen, brachliegenden Fläche. Im Park und in den umliegenden alten Gärten wimmelte es von Hausspatzen. Die Speisezettel dieser Eulen waren äusserst merkwürdig und gut in Übereinstimmung mit der merkwürdigen Beschaffenheit des Jagdreviers (Tabelle 8).

7. Ein anderes Beispiel, das zeigt dass Sperlinge öfters stark von den Eulen zu leiden haben, ist in Tabelle 12 dargestellt. Der betreffende Eulentrupp hielt sich im Winter 1931-'32 während einiger Monate in der unmittelbaren Nähe der Stadt Haag auf, wo ein fast unbegrenzter Spatzenbestand vorhanden war. Obwohl hier die Eulen auch verhältnismässig viele Säugetiere schlugen, machten die Vögel und unter diesen die Spatzen einen grossen Teil der Nahrung aus (Tabelle 12).

8. In derselben Tabelle 12 fällt eine andere Besonderheit auf: die Zahl der Zeisige ist sehr hoch. Dieses Gebiet ist bei uns als Aufenthaltsort vieler Zeisigtrupps bekannt; neben dem Eulenbestand befindet sich ein Erlenbusch, wo man im Winter die Zeisige fast nie vergebens zu suchen braucht.

9. Das in der Tabelle 10 unter "Winter 1931-'32" behandelte Gebiet weist unter den Vögeln einen sehr hohen Finkenprozentsatz auf. In unserer Übersicht (Tabelle 1) nehmen die Finken mit 612 unter 3262 Vögeln etwa

19% ein, in unserem Finkengebiet nehmen sie mit 235 unter 705 Vögeln 33% ein. Dieses Gebiet ist in der Tat im Winter von Finken dicht besiedelt und wenn man beim Sonnenuntergang das Wäldchen besucht, sieht und hört man überall Finken, die vor dem Schlafengehen noch während einer halben Stunde in kleinen Trupps umherfliegen.

Diese Beispiele mögen genügen um zu zeigen, dass, immer wenn es uns möglich war ein mit einer Tierart auffällig stark besiedeltes Gebiet auf die Nahrung seiner Waldohreulen zu prüfen, es in jedem einzelnen Fall möglich war, auch in der Nahrung der Eulen einen ungewöhnlich hohen Prozentsatz dieser Tierart nachzuweisen. Es ist dies für Maulwürfe, Spitzmäuse, Hausmäuse, Waldmäuse, Wühlmäuse, Hausspatzen, Finken und Zeisige nachgewiesen worden.

B. Übereinstimmende Abweichung der Nahrung bei Waldohreulen und anderen Raubvögeln s.l.

1. Wie schon unter A.4 mitgeteilt, frassen die walcherschen Eulen besonders viele Hausmäuse (Tabelle 9). Die Möglichkeit, dass wir es hier mit einer zufälligen Übereinstimmung zu tun haben, wird geringer, wenn wir sehen, dass auch die sich hier aufhaltenden Schleiereulen, von denen wir einen kleinen Gewöllfund untersuchen konnten, anormal viele Hausmäuse erbeuteten. Unter 123 Beutetieren der Schleiereulen fanden sich hier 39 Hausmäuse. Vergleichen wir dieses mit einem anderen Gebiet, z.B. Texel, wo wir ebenfalls einige Schleiereulengewölle untersuchen konnten, so ergibt sich ein grosser Unterschied. Die texelschen Schleiereulengewölle enthielten: 96 Microtus ratticeps, 39 Wasserspitzmäuse, 5 Hausmäuse, 30 Waldmäuse und eine Wanderratte.

2. Unter A.5 gab ich die ziemlich stark abweichenden Speisezettel der Harderwijker Eulen. Am auffälligsten waren hier die 5 Maulwürfe. Auch in diesem Fall besteht eine überrasschende Übereinstimmung zwischen der Eule und einem anderen Räuber, in diesem Fall dem Baumfalken (Falco subbuteo). Die normale Nahrung des Baumfalken besteht aus Vögeln und Insekten; Säugetiere sind ganz selten angetroffen worden, so selten dass man noch nicht darüber einig ist, ob der Baumfalke sich seine Säugetiere tatsächlich selber zu erbeuten vermag. An anderer Stelle (69) teilte ich die merkwürdige Zusammenstellung der Nahrung der betreffenden Baumfalkenbrut mit. Der alte Baumfalke (das ♂ besorgte hier die Herbeischaffung der Nahrung für die ganze Familie) jagte in demselben Küstengelände wie die Waldohreulen, wie wir es durch direkte Beobachtung an beiden Arten unzweideutig feststellen konnten. In Zusammenhang hiermit brachte das ♂ sehr viele Vögel und—auch an ganz schönen Tagen, wenn die Gegend von allerhand Insekten wimmelte—sehr wenig Insekten. Daneben brachte er nun auch Säugetiere, und so konnten die Reste von 6 Maulwürfen, 3 Spitzmäusen

und 1 Feldmaus nachgewiesen werden. Dieser Fall zeigt also eine deutliche übereinstimmende Abweichung bei dem Baumfalken und der Waldohreule.

Obwohl ich über eine dichte Besiedelung mit Spitzmäusen in diesem Gebiet nur fragmentarische Beobachtungen habe, sei hier auf den übereinstimmenden hohen Spitzmausgehalt der Nahrung beider Vögel hingewiesen. Auch hier verringert die übereinstimmende Abweichung die Möglichkeit, dass es sich bei der Waldohreule etwa um einen "Spitzmäusespezialisten" handelt.

3. Was die Vogelnahrung anbetrifft, so konnten wir in einzelnen Fällen einen Vergleich zwischen Waldohreule und Sperber anstellen. Der Sperber rupft, wie es Uttendörfer ausführlich in seinen "Studien" (72) darstellt, seine Beute gerne im Stangenholz auf dem kahlen Boden. Oft sind hierdurch die Eulenbestände zu gleicher Zeit günstige Sperberrupfplätze.

An anderer Stelle (71) teilen wir mit, wie die in den holländischen Nordseedünen überwinternden Sperber eine ähnliche Abhängigkeit von der Zusammenstellung des Milieus zeigen wie die Waldohreulen. Wir behandeln dabei auch die übereinstimmenden Funde, die wir an Sperber und Waldohreule machten. Da diese Beobachtungen in holländischer Sprache mitgeteilt sind, bespreche ich sie hier abermals.

In demselben Gebiet, wo unsere Waldohreulen viele Haussperlinge erbeuteten (vgl. Tabelle 12), haben die Sperber sich auch an Spatzen gütlich getan. Während in unseren Sperberfunden die Hausspatzen mit 61 unter 832 Vögeln, d.h. mit ca 7% vertreten sind, fanden wir im "Spatzengebiet" unter 92 Vögeln 18 Spatzen, d.h. ca 20% (Tabelle 13).

4. Ähnlich steht es um die Zeisige. In Tabelle 13 sind in ähnlicher Weise wie für den Haussperling die verschiedenen Werte für die Zeisige wiedergegeben. Also auch hier wieder eine weitgehende Übereinstimmung zwischen Waldohreule und Sperber.

5. Unter A.9 beschrieb ich ein reiches Finkengebiet. Die Eulen schlugen hier unter 705 Vögeln 235 Finken (und Bergfinken), d.h. 33% der Vögel. Der Durchschnittswert der Finken in unserer Übersicht ist 19%. Beim Sperber liegen die Verhältnisse wieder ähnlich, wie aus der Tabelle 14 ersichtlich ist.

Diese weiteren fünf Beobachtungen zeigen, dass wir es in den unter A. mitgeteilten Fällen, wo eine übereinstimmende Abweichung in Eulennahrung und Milieu festzustellen war, nicht mit Zufallserscheinungen zu tun haben.

Es bleibt nach diesen Beobachtungen noch die Möglichkeit bestehen, dass diese Abweichungen dadurch zustande kommen, dass die Eulen usw. die einen Vorzug für Spatzen haben (d.h. geltend machen!), sich im Spatzengebiet ansiedeln, die Spitzmäuse-"Spezialisten" in Spitzmausgebieten und so weiter. Diese Möglichkeit fällt aber weg, wenn wir sehen, dass auch die zeitlich bedingten Schwankungen in dem vorhandenen Nahrungsvorrat eines und desselben Gebietes einen ähnlichen Einfluss auf die Nahrung der Eulen

haben. Die in dieser Hinsicht von uns gesammelten Beobachtungen seien jetzt näher betrachtet.

C. Zeitlich bedingte Schwankungen in der Zusammenstellung der Nahrung

1. Es geht aus den ersten 4 gegebenen Tabellen zur Genüge hervor, dass bei weitem das wichtigste Beutetier *Microtus* ist, die Feldmaus. Die kleinen Rodentier aus der "Niche" (Elton, 15) der Felmäuse stellen, wie z.B. die Blattläuse, eine Universalnahrung da, oder wie Elton sagt, eine "Key-industry," welche grosse Mengen von Pflanzen festgelegte Energie für die karnivore Tierwelt entschliesst. Nun unterliegt der Bestand dieser Rodentier in den verschiedensten Teilen der Erde sehr starken Schwankungen. Am bekanntesten sind diese bei den Lemmingarten, aber auch bei den verschiedenen *Microtus*-arten sind sie sehr auffällig. Ich komme weiter unten (Abschnitt IX) noch hierauf zu sprechen. Ein Charakterzug der *Microtus*-schwankungen ist die Tatsache, dass sie über grosse Gebiete ungefähr gleichzeitig verlaufen. So hat in ganz Nordwesteuropa das Jahr 1930 eine Feldmäusekalamität gebracht, die auch in unserem Land—obwohl schwach—bemerkbar war. Der Bestand nahm im Sommer 1930 überrasschend schnell zu, blieb im Herbst und Winter hoch und fiel im nächsten Frühling und im Sommer allmählich, worauf der Bestand im Winter 1931-'32 verhältnismässig niedrig war. Diese Bestandsschwankungen der Feldmäuse in Holland sind durch eine Enquête mit genügender Genauigkeit nachgewiesen worden (siehe Abschnitt IX A).

Nun haben wir verschiedene Gebiete während längerer Zeit unter Kontrolle gehabt, sodass wir die Nahrung der Eulen über verschiedene Perioden vergleichen können. Es zeigte sich, dass in der Nahrung der Eulen dieser verschiedenen Gebiete die Bestandsschwankung deutlich bemerkbar ist; dies ist aus den Tabellen 15 bis 19 ersichtlich. Überall sehen wir im Winter 1930-'31 ein deutlich ausgeprägtes Maximum der Feldmäuse, auf welches allmähliche Abnahme folgte.

In der Literatur finden wir mehrere Angaben über die Ernährung der Waldohreulen während starker Mäuseplagen, so bei Uttendörfer (72), Csörgey (11) und Dobbrick (12). Die Häufigkeit der Feldmäuse korreliert dann immer mit dem Feldmäusegehalt der Nahrung. Es lassen diese einzelnen Beobachtungen aber noch immer die Möglichkeit verschiedener Erklärungen offen und daher schien es mir erwünscht, die Nahrung der Eulen und die Schwankungen im Feldmausbestand zu gleicher Zeit durchzubeobachten.

Es zeigt sich also bis jetzt, dass die Bestandsschwankungen der Feldmäuse in allen untersuchten Fällen den gleichen Einfluss auf die Zusammenstellung der Nahrung der Waldohreulen haben. Es soll hierbei noch ausdrücklich betont werden, dass, obwohl in Zeiten starker Feldmäusekalami-

tät die Feldmäuse in beliebiger Menge zu haben sind (man lese die Beschreibungen der unglaublichen Unmengen z.B. bei Maxwell (44) und bei Tantzen (65)), die Nahrung doch nie ausschliesslich aus Feldmäusen besteht.

2. An anderer Stelle berichtete ich schon (68), dass ich im Sommer des Jahres 1931 bei einer Eule eine auffällige Änderung in der Zusammenstellung der Nahrung innerhalb kurzer Zeit feststellte und interpretieren konnte (siehe die Tabelle 20). Die betreffende Eule jagte regelmässig, wie durch direkte Beobachtung festgestellt wurde, über eine Acker- und Wiesenlandschaft. Vor dem 1. August waren die Speisezettel sehr vielseitig: Maulwürfe, Spitzmäuse, Wasserratten und Vögel wurden verhältnismässig sehr oft erbeutet. Der Feldmausgehalt war nicht höher als ± 50 %. Um den 1. August herum fiel die Ernte des Getreides, wodurch die Feldmäuse in eine ihren Raubfeinden gegenüber äusserst ungünstige Lage versetzt wurden. Die nach dem 1. August untersuchten Gewölle, die zwar gering an der Zahl sind, zeigen einen sehr viel höheren Feldmäuseprozentsatz, nämlich ca 90%.

Diese Beobachtung ist darum wichtig, weil es sich hier mit absoluter Sicherheit um eine Änderung in der Nahrung derselben Eule handelt, denn es ist die Geschichte einer Eulenbrut, und die allerdings flüggen Jungen blieben während voller zwei Monate an der Stelle und liessen sich von den Alten ernähren.

Es zeigt sich nun weiter, dass auch Schwankungen in dem Bestand anderer Beutetiere dieselben, parallel verlaufenden Schwankungen in der Nahrung zur Folge haben.

3. Die Wanderratte wird von der Waldohreule gewöhnlich in nicht grosser Anzahl erbeutet. Im Sommer des Jahres 1931 wurde aus verschiedenen Teilen des Landes eine Zunahme der Wanderratten gemeldet, im Herbst wurden sogar von den Behörden der Stadt Leiden offiziell Massregeln getroffen einer Plage vorzubeugen.

Es ist auch von allgemein ökologischem Gesichtspunkt aus eine interessante Tatsache, dass diese Rattenkalamität um ein Jahr später kam als die Feldmäusekalamität. Vielleicht handelt es sich hier um verwandte Phänomene.

Diese Zunahme machte sich in der Nahrung der Waldohreulen bemerkbar. Um dieses zu zeigen gebe ich eine Übersicht über die Säugetiernahrung einiger Waldohreulentrupps, die sich in einer Dünenlandschaft nicht weit vom Haag aufhielten, wobei die Feldmäuse ausser Acht gelassen sind, um einen Einfluss ihrer Bestandsschwankungen auszuschalten. So finden wir hier im Herbst und Winter 1930-'31 19 Wanderratten auf 362 andere Säuger (exklusiv *Microtus*) und im Herbst und Winter 1931-'32 80 Wanderratten auf 816 andere Säuger, d.h. doppelt so viel (5% resp. 10%).

4. Schliesslich haben Schwankungen in dem Bestand einer Vogelart denselben Einfluss auf die Zusammenstellung der Nahrung. Ein schönes Beispiel stellten wir im März 1931 fest. In einem unserer Waldohreulengebiete

stellten sich um diese Zeit plötzlich viele Wacholderdrosseln ein. Während 14 Tage fanden sich dementsprechend viele von den Eulen herrührende Rupfungen dieser Vögel (Tabelle 21).

D. Übereinstimmende, zeitlich bedingte Schwankungen in der Nahrung der Waldohreule und anderer Raubvögel.

1. Der Einfluss der Feldmäusekalamitäten auf die Nahrung verschiedener Eulen ist schon oft klar dargestellt worden, so z.B. für die Sumpfeule von Maxwell (44) und Uttendörfer (72), für die Schleiereule vor allem von Schneider (57) und Guérin (26), in 1930 von Uttendörfer (74). Im IX. Abschnitt kommen auch andere Vögel noch zur Sprache.

2. Der unter C.5 mitgeteilte Fall, wo eine Invasion von Wacholderdrosseln die Nahrung der Waldohreulen beeinflusste, konnte auch in Bezug auf die Nahrung der Sperber des betreffenden Gebietes näher analysiert werden. Die zahlenmässige Steigerung der von den Sperbern erbeuteten Wacholderdrosseln ist in der Tabelle 21 wiedergegeben.

VI. DIE URSACHEN DER ÖRTLICH UND ZEITLICH BEDINGTEN SCHWANKUNGEN IN DER ZUSAMMENSTELLUNG DER NAHRUNG

Im vorigen Abschnitt haben wir einige Beobachtungen gegeben, die alle eine Übereinstimmung zwischen den Schwankungen in der Nahrung der Eulen und denen in der Umgebung der Eulen ergaben. Da diese Beobachtungen in einer für den Leser vielleicht etwas langweiligen Form wiedergegeben sind, fasse ich sie zusammen:

A. Wenn die Zusammenstellung der Fauna eines Gebietes in auffälliger Weise vom Durchschnittlichen abwich, indem ein Beutetier in auffallend grosser Zahl vertreten war, stellten wir eine übereinstimmende Abweichung in den Speisezetteln der Eulen fest, und umgekehrt. Unsere Beobachtungen betreffen Waldmäuse, Feldmäuse, Spitzmäuse, Hausmäuse, Maulwürfe, Hausspatzen, Finken und Zeisige.

B. Wenn es in solchen Fällen möglich war, auch die Nahrung anderer Räuber hieraufhin zu untersuchen, so konnten wir übereinstimmende Abweichungen feststellen. Unsere diesbezüglichen Beobachtungen betreffen: Hausmäuse (Schleiereule), Maulwürfe (Baumfalke), Spitzmäuse (Baumfalke), Hausspatzen (Sperber), Finken (Sperber) und Zeisige (Sperber).

C. Zeitlich bedingte Schwankungen in dem Bestand eines Beutetieres haben ähnliche Schwankungen in der Nahrung der Eulen zur Folge. Dieses konnten wir an Feldmäusen, Wanderratten und Wacholderdrosseln beobachten.

D. Die Zunahme der Feldmäuse zeigt sich auch in der Nahrung der Sumpfeule und der Schleiereule, die beschriebene Wacholderdrosselninvasion machte sich auch in der Nahrung der Sperber bemerkbar.

Wie ich im vorigen Abschnitt darzutun versucht habe, kann die Möglichkeit eines individuellen Bevorzugens nur durch Beobachtungen wahrscheinlich gemacht werden, welche zeigen, dass ein hoher Gehalt eines bestimmten Beutetieres in der Nahrung nicht mit einer hohen Anzahl der vorhandenen und erreichbaren Tiere Hand in Hand geht. Gelingt es uns nicht solche Abweichungen zu finden, und finden wir dagegen immer nur Übereinstimmungen zwischen Nahrung und Milieu, so bleibt nur die Möglichkeit offen, dass die Raubvögel nehmen, was ihnen begegnet ohne einen individuellen Vorzug geltend zu machen; wobei dann die Möglichkeit einer Gewohnheitsbildung an gewisse Jagdreviere offengelassen werden muss.

Angesichts der im vorigen Abschnitt mitgeteilten vergleichenden Beobachtungen müssen wir also darauf schliessen, dass die zeitlich und örtlich bedingten Schwankungen in der Zusammenstellung der Nahrung unserer Waldohreulen auf dieselbe Ursache zurückzuführen sind, d. h. dass sie immer von übereinstimmenden Schwankungen in dem erreichbaren Nahrungsvorrat verursacht werden. Eine Gewohnheitsbildung destimmten Gebieten gegenüber ist mit diesen Tatsachen vor Augen nur zu verstehen, wenn diese Gewohnheitsbildung von Nahrungsüberfluss bedingt wird, sonst müssten wir ja Abweichungen zwischen Nahrung und Milieu finden. Ausserdem nimmt die Eule auch in solchen Gebieten, was eben vorhanden ist und was ihr begegnet, denn selbst unter den allergünstigsten Bedingungen besteht die Nahrung nie aus nur einer Art, immer werden auch noch andere Arten gefressen, sei es in geringer Zahl.

Während Feldmauskalamitäten oder während örtlich auftretender grosser Ansammlungen bestimmter Beutetiere (Vogelzug) werfen die Eulen sich auf diese Tiere, *nicht weil es eben diese Tiere anbetrifft, sondern nur weil es deren viele sind.*

Eine solche Gewohnheitsbildung kommt zweifelsohne viel vor, ja wir können m.E. mit Recht behaupten, dass das Überwinterungsverhalten unserer Eulen ohne eine solche überhaupt nicht so gestaltet sein würde, wie es ist.

Uttendörfer hat beim Sperber vermutlich viele Beispiele gefunden. Es gibt Sperber, die hauptsächlich in den Ortschaften jagen, auch solche, die auf der Feldflur jagen, andere Sperber desselben Gebietes sind Waldsperber. Man vergleiche auch Seite 511-512.

Diese Schlussfolgerung ist vom psychologischen Standpunkt aus betrachtet ziemlich unerwartet. Sie bedeutet, dass man an Stelle einer Waldohreule ebensogut eine, zwar technisch äusserst raffinierte, Vogel-und-Maus-Greifmaschine in die Biozönose stellen könnte.

Es fehlte mir die Zeit mich genügend psychologisch zu orientieren, um über diese Verhältnisse bei anderen Tiergruppen ein Urteil zu gewinnen. Ich sah nur einen Beitrag von Brooker Klugh (9) über die Ökologie des amerikanischen "Red Squirrel" (*Sciurus hudsonicus*), wo ein individueller Vorzug für bestimmte Nahrung erwähnt

wird. Wahrscheinlich sind die Beobachtungen von Hauchecorne (*27*) am Maulwurf ähnlich zu deuten.

Steven (64) hat eine ausführliche quantitative Untersuchung über die Nahrung 29 verschiedener Nordseefische in der Nähe von Plymouth publiziert. Seine sehr sorgfältigen Beobachtungen weisen aus, dass jeder Fisch dasjenige aus seiner Umgebung frisst, was er mit seiner angeborenen Jagdweise erbeuten kann. Die Nahrung jeder einzelnen Art ist in verschiedenen Biozönosen verschieden; diese Unterschiede sind alle von der Zusammenstellung des Milieus bedingt. Hier haben wir es also allem Anschein nach mit einem durchaus ähnlichen Fall zu tun wie bei den Waldohreulen.

Was nun meine Schlussfolgerung über die Eulen anbetrifft, so sei sofort bemerkt, dass ich mir von ihrer geringen psychologischen Tragweite sehr wohl bewusst bin. Die Methodik lässt eine Schlussfolgerung von ökologisch genügender Tragweite zu, und dieses ökologisch hinreichend begründete Resultat hat einen psychologischen Hintergrund, aber wir können auf Grund unserer Feldbeobachtungen nicht behaupten, dass es nicht psychologisch noch wichtige, zwar ökologisch zu vernachlässigende, kleine Abweichungen gäbe, die durch individuellen Vorzug verursacht wären. Hierüber könnten uns nur experimentelle Untersuchungen im Laboratorium und vermutlich auch Feldwerk mit verfeinerten Methoden ein Urteil ermöglichen.

Betrachten wir jetzt noch kurz die ökologischen Konsequenzen unserer Resultate. Sie zeigen, dass die Waldohreule einen ausgleichenden, nivellierenden Einfluss auf die Bestände ihrer verschiedenartigen Beutetiere hat. Dass es ihr nie gelingt, diese Bestände wirklich vollkommen zu nivellieren, ist sozusagen nicht ihre Schuld, und ich verstehe denn auch nicht, weshalb Schnurre (58) beim Sperber—der sich, wie wir an anderer Stelle mitgeteilt haben, in dieser Hinsicht ganz ähnlich verhält—nicht von einer ausgleichenden Rolle reden will. Es ist eben das ökologisch wichtigste Kennzeichen der Ernährungsbiologie dieser Vögel, dass sie eine ausgleichende Wirkung ausüben!

Wenn unter den Beutetieren eine Art zahlenmässig plötzlich stark zunimmt, wirkt unsere Eule nivellierend, nicht nur indem sie dann mehr Individuen dieser Art erbeutet, sondern auch dadurch dass sie die anderen Arten weniger nachstellt. Nimmt dagegen eine Art an Häufigkeit ab, so stellt die Eule nicht nur dieser Art weniger nach, sondern ist gezwungen, sich mehr von den anderen Arten zu nehmen. So macht sie ihren doppelten, sogar vierdoppelten Schnitt! Wir sehen jetzt auch, dass ein genaues Studium der Ernährung der Waldohreule den Beweis dafür erbringt, dass sie *nie* ein Beutetier auszurotten imstande ist! Dasselbe erfolgt sicher auch für unsere anderen Raubvögel.

Von der anderen Seite betrachtet, trifft es uns, wie vorteilhaft diese höchst vollkommne Polyphagie für die Eule ist. In schroffem Gegensatz mit einem monophagen Karnivoren, der ganz und gar von der veränderlichen Population seines einzigen Beutetieres abhängig ist, verfügt sie immer über

verschiedene, manchmal sogar zahlreiche, unabhängig voneinander fluktuierende Populationen, wodurch die Aussicht auf Nahrungsarmut und somit auf Beeinträchtigung des Artbestandes äusserst gering ist.

VII. DIE ABHÄNGIGKEIT VOM MILIEU BEI ANDEREN EULEN UND BEI RAUBVÖGELN

Die an der Waldohreule gewonnenen Ergebnisse nötigen zu einer näheren Betrachtung einiger anderen Eulen und Raubvögel. Die Nahrung mancher unserer einheimischen Eulen und Raubvögel ist schon eingehend studiert worden; ich weise wieder an erster Stelle auf Uttendörfer hin; für eine sichere Beurteilung der Beziehungen zwischen Nahrung und Umwelt reichen die Beobachtungen jedoch meistens noch nicht aus. Es gibt aber viele Anzeigen, dass wir es hier überall mit demselben Phänomen zu tun haben.

Die Schleiereule *(Tyto alba)* ist die am eingehendsten auf ihre Nahrung untersuchte Eule. Obwohl sie sehr viele Spitzmäuse frisst und verhältnismässig weniger Wühlmäuse als die Waldohreule, machen sich die Schwankungen im Feldmäusebestand in ihrer Nahrung stark bemerkbar. Die sorgfältigsten Beobachtungen hierüber verdanken wir Guérin (26) und Uttendörfer (72, 74). Aus diesen, sich über viele Tausende von Beutetieren erstreckenden Untersuchungen geht klar hervor, dass die Schleiereule sich, den Feldmäusen gegenüber, ähnlich wie die Waldohreule verhält. Unterschiede zwischen beiden Arten in anderer Hinsicht werden im nächsten Abschnitt behandelt. Die oben schon mitgeteilte Beobachtung, dass die Schleiereule auch in einem Revier, das mit Hausmäusen dicht besiedelt war, viele Hausmäuse frass, zeigt dass wir es hier auch mit einer allgemein begründeten Regelmässigkeit zu tun haben.

Die Sumpfeule *(Asio flammeus)* ernährt sich im Allgemeinen mit denselben Beutetieren wie die Waldohreule (vgl. Uttendörfer (72)). In Feldmäusejahren besteht auch die Nahrung dieser Eule hauptsächlich aus Feldmäusen; dies wird schon deutlich von Maxwell (44) beschrieben (vgl. auch Elton (14) und Hudson (33)) und neuerdings hat Gerber (23) eine den Zusammenhang zwischen Mäuseplage und Nahrung zeigende Beobachtung veröffentlicht.

Der Sperber *(Accipiter nisus)* ist oben schon öfters zum Vergleich herangezogen worden. Ich kann mich daher jetzt kurz fassen. Die brauchbarsten Beobachtungen finden sich bei Uttendörfer (72, 73) und bei Kramer (39); Schnurre (58) beschreibt eine reichhaltige, sorgfältige Beobachtung und wir konnten selber an anderer Stelle Beobachtungen über ziehende und überwinternde Sperber im holländischen Dünengebiet mitteilen (71). Die meisten Beobachtungen scheinen in derselben Weise gedeutet werden zu müssen, wie ich es hier bei der Waldohreule aufzuzeigen versucht habe. Dadurch aber dass Uttendörfer meistens keine genauen vergleichenden

Beobachtungen über Nahrung und Umwelt mitteilt, reichen die meisten seiner Beobachtungen, wie gesagt, zur Beantwortung der vorliegenden Frage nicht aus. Aus demselben Grund sind auch die Beobachtungen, auf deren Grund Uttendörfer auf richtige "Spezialisten" schliessen zu müssen glaubt, m.E. hierfür nicht hinreichend.

Sichere Daten über eine Übereinstimmung zwischen der Vermehrung eines Beutetieres in der Umwelt und in der Nahrung des Sperbers betreffen folgende Tierarten: Feldmaus (Kramer, 39), Kohl- und Blaumeise, Trauerfliegenschnäpper (Schnurre, 58), Erlenzeisig, Buntspecht, Kreuzschnabel (Uttendörfer, 74), Buchfink, Erlenzeisig, Hausspatz, Star, Wasserralle, Wacholderdrossel, Weindrossel und Teichhuhn (Tinbergen, 71). So ist der Sperber nach der Waldohreule der hinsichtlich unserer Frage am besten untersuchte Vogel.

Vom Habicht *(Accipiter gentilis)* berichtete ich schon, wie ein überwinterndes Exemplar in der Hauptsache Krähen schlug, die in der Nähe in Mengen zu haben waren. Als der Frühjahrszug der Kiebitze anfing und die Brutvögel dieser Art in den benachbarten Wiesen eintrafen, erbeutete der Habicht bis zu seinem Abzug eine Anzahl Kiebitze (66).

Über den Baumfalken *(Falco subbuteo)* teilte ich an anderer Stelle schon eine Beobachtung mit, die deutlich den Einfluss der Zusammenstellung des Jagdreviers auf die Speisezettel zeigt (69). Es handelte sich hier nicht bloss um Vögel, sondern auch um Maulwürfe und Spitzmäuse.

Unsere Beobachtungen an anderen Raubvögeln und Eulen sind noch zu lückenhaft um hier mitgeteilt werden zu können.

Die hier mitgeteilten Tatsachen sind für die meisten Arten noch sehr unvollständig. Sie deuten aber alle daraufhin, dass die betreffenden Vögel sich im Grunde ähnlich wie die Waldohreule verhalten. Eine sichere Beurteilung wird aber erst dann möglich sein, wenn für jede Art eine Reihe von Angaben über die Ernährung unter den verschiedensten Bedingungen vorliegt, wobei jedesmal die Abhängigkeit von diesen Umweltsbedingungen geprüft worden ist.

VIII. DIE BEZIEHUNGEN ZWISCHEN *ASIO O. OTUS* UND DEN *MICROTUS*-ARTEN

A. Die Bestandsschwankungen der Feldmäuse

Oben zeigte sich, dass der Feldmäuseprozentsatz der Nahrung erheblichen Schwankungen unterworfen war. Diese Schwankungen verliefen parallel—so weit sich das sagen lässt—mit den Bestandsschwankungen der Feldmäuse selbst. Weil diese Bestandsschwankungen ein sehr interessantes ökologisches Phänomen darstellen, ist es angebracht sie näher zu betrachten, bevor wir uns ein Urteil über die Beziehungen *Asio-Microtus* bilden.

Die Bestandsschwankungen der Feldmäuse sind schon sehr lange bekannt.

Die starken Maxima sind als Plagen den Menschen immer am meisten aufgefallen. Der erste aber, der die ökologischen Gesetzmässigkeiten aufzudecken suchte, war Elton (14-18). Elton lenkte die Aufmerksamkeit auf zwei Tatsachen, die es ermöglichen über die Ursachen der Bestandsschwankungen Näheres zu erfahren. Erstens zeigen die Maxima—auch diejenigen anderer Rodentier—eine überraschend regelmässige Periodizität. Die Zeitdauer zwischen zwei verschiedenen Perioden beträgt durchschnittlich 3, oder 4 Jahre. Zweitens treten die Maxima manchmal über grössere Gebiete zu gleicher Zeit auf, wie z.B. 1875, 1891-'93 und 1900.

Elton bemerkt hierzu: "Such facts would be explained by the hypothesis that there was some climatic factor widely, such as that caused by solar changes." Von den Faktoren, die den Feldmäusebestand beeinträchtigen, ist wenig bekannt. Die Bauern wissen, dass ein trockener Sommer viele, ein nasser Sommer wenige Mäuse bringt. Dieses ist für die regelmässige Periodizität jedoch nicht entscheidend, denn der bei uns nasse Sommer 1930 hat doch ein Maximum gebracht, das zwar vermutlich von der Nässe stark gedrückt wurde. Starker Frost ohne Schnee tötet viele Mäuse.—Soweit experimentelle Untersuchungen vorliegen, erlauben diese uns aber noch keinen Einblick in die Ursachen der Bestandsschwankungen. Man vergleiche für eine eingehendere Besprechung der Probleme Elton (14, 17). Über die Rolle der Raubfeinde siehe weiter unten.

In den letzten Jahren hat Middleton (45, 46) in England und Schottland neue Beobachtungen gesammelt. Middleton zeigt zwischen 1892 und 1926 neun, durch vierjährige Perioden geschiedene Maxima. Dieses bestätigt also Elton's Annahme. Von den letzten Jahren hat er genaue Daten über den Verlauf der Schwankungen gesammelt, und dabei zeigte es sich, dass obwohl das Jahr 1930 in vielen Gegenden ein Mäusemaximum war, es auch Gebiete gab, wo im Jahre 1930 eine Abnahme seit 1929 festzustellen war. Dieses Resultat war insofern überraschend, als es zeigte, dass die Maxima nicht überall gleichzeitig aufzutreten brauchen d.h. lokal sich verfrühen können. Es war also nicht bloss für unsere Eulenstudien, sondern auch in mehr allgemein ökologischer Hinsicht interessant zu wissen, wie die Bestandsschwankung der Feldmäuse im Jahre 1930 in Holland vor sich ging.

Die beiden beigefügten Karten (Abb. 8 u. g.) sind nach etwa 1000 auf eine Enquête eingetroffenen Antworten zusammengestellt. Unter Mitwirkung des "Plantenziektenkundige Dienst" zu Wageningen, Holland,[2] wurde ein so objektiv als möglich aufgestellter Fragebogen herumgesandt; die Antworten wurden kritisch verwertet. Dieses war um so einfacher, als die Antworten aus bestimmten Gegenden im Allgemeinen sehr gleichlautend waren. Es zeigte sich, dass fast überall im Sommer 1930 eine Zunahme beobachtet wurde und eine allmähliche Abnahme im Frühjahr 1931 anfing, die jedenfalls bis Ende 1931 anhielt. Es scheint, dass auch in Holland an manchen Stellen das Maximum schon 1929 gefallen ist.

[2] Gerne spreche ich Herrn Ir. N. Van Poeteren, Direktor des "Plantenziektenkundige Dienst" für seine Unterstützung meinen verbindlichsten Dank aus.

Ausser in Holland und England ist im Jahre 1930 auch in Deutschland (vgl. z.B. Tantzen (65), Gerber (23), Kramer (39)), Ungarn (vgl. von Kálmán (36), Kabáczy (35), Kiss (37), H. Schenk (54)), und Luxemburg (Uttendörfer, 74) ein Maximum der Feldmäuse beobachtet worden, das sich in vielen Gegenden zu einer richtigen Plage entwickelte.

B. Die Raubfeinde der Feldmäuse, ihr Einfluss auf den Feldmäusebestand

Die Feldmäuse stellen in der Natur, wie gesagt, eine Art Universalnahrung dar. Wie verschiedene andere, namentlich pflanzenfressende Tierarten sind die Feldmäuse sehr allgemein verbreitet, vermehren sie sich stark und werden von vielen Räubern gefressen.

Über die Raubfeinde der Feldmäuse finden wir mehrere Angaben in der Literatur, die uns nicht nur zeigen, dass die betreffenden Arten Feldmäuse fressen, sondern auch, dass sie während starker Feldmauskalamitäten grosse Mengen Feldmäuse verschlingen können, sich also ähnlich wie die schon besprochenen Eulen in "Mäusejahren" auf die Feldmäuse werfen. Es lohnt sich die diesbezüglichen Angaben, denen ich bei der Durchsicht der Literatur begegnete, zusammenzufassen, wobei allerdings kein Anspruch auf Vollständigkeit gemacht werden kann.

R. Service (61) gibt die Viper als Mäusefresser an. Während der Mäuseplage in Schottland in den Jahren 1891 und '92 wurden Exemplare mit 3, sogar 5 Feldmäusen im Magen gefunden. Der Fuchs ist als Mäusevertilger bekannt genug (vgl. Elton (14), Krumbiegel (40)), das grosse und das kleine Wiesel sind nach Maxwell (44), Middleton (45) und Krumbiegel (40) tüchtige Mäusejäger, sie vermehren sich in Feldmäusejahren manchmal sehr stark, richten sich dann bei plötzlicher Abnahme der Feldmäuse auf andere Nahrung und können so grossen Schaden im Hühnerstall verursachen (vgl. Middleton (45)). Über die Wanderratte bemerkt Krumbiegel (40): ". . . dass sogar die räuberische *Epimys norvegicus* lokal als Vertilgerin von Mäusen nützlich wurde." Unter den Insektivoren scheinen sich tüchtige Mäusejäger zu befinden; Krumbiegel sagt hierüber (40): "Eine bei ihrer Individuenzahl weit verbreitete Nahrung stellen die Muriden dar, welche *Crocidura* und *Sorex*, den Musteliden, *Erinaceus*, sämtlichen Carnivoren, evtl. auch *Talpa* zur Nahrung dienen." Über *Talpa* vergleiche man auch Hauchecorne (27).

Unter den Vögeln finden sich viele Mäusejäger. Der Fischreiher (Tantzen (65), H. Schenk (54), E. Nagy (48), von Fernbach (20), Tinbergen (67)) frisst regelmässig Feldmäuse, sei es in geringer Zahl. In Mäusejahren ist beobachtet worden, wie er in grösseren Gesellschaften wochenlang auf Feldmäuse jagte. Ähnlich macht es nach Vasvári (76) und H. Schenk (54) der Purpurreiher; nach Vasvári (75) frisst auch die Rohrdommel ziemlich viele Feldmäuse. Tantzen (65) und von Kálmán beschreiben wie weisse Störche während Feldmäusekalamitäten in grossen Trupps der Mäusejagd obliegen. Die Beobachtungen von Kálmán's (36) geben einen guten Eindruck davon, wie viele Mäuse diese Vögel zu verschlingen imstande sind. Mit dem Mähen eines Kleefeldes wurde morgens früh ein Anfang gemacht. Um elf Uhr waren auf dem frischgemähten Stück 154 Störche mit der Feldmäusejagd beschäftigt. Einer dieser Störche wurde während einer Stunde ununterbrochen beobachtet: er frass 44 Mäuse, 2 junge Hamster und 1 Frosch! Ein Gewölle nach dem anderen wurde ausgeworfen.—

Diese Beobachtung ist auch darum für uns wichtig, weil dieser Storch nicht *nur* Feldmäuse frass (obwohl diese hier doch in hinreichender Menge vorhanden waren!), sondern auch zwei junge Hamster und einen Frosch. Also auch hier wieder: "nicht weil es eben diese Tiere anbetrifft, sondern nur weil es deren viele sind." (s. oben S. 521)— Nach Uttendörfer (*72*) besteht die Hauptnahrung der Wiesen—, Korn— und Rohrweihe, sowie die des Schreiadlers (vgl. auch Siewert (*62*)), aus Feldmäusen. Beim Bussard liegen die Verhältnisse ähnlich, nach den Untersuchungen Uttendörfer's (*72*), Eckstein's (*13*), Rörig's (*53*) und Greschick's (*24*). Der Sperber frisst nach Uttendörfer (*72*) regelmässig Feldmäuse; in Mäusejahren sogar in grosser Anzahl, wie von Fernbach (*19*) erwähnt und wie es Kramer (*39*) neuerdings an mehreren sorgfältig kontrollierten Sperberbruten festgestellt hat. Der Turmfalke ist neben den Eulen und den Musteliden einer der ärgsten Feldmäusefeinde (Uttendörfer (*72*), Rörig (*53*)); nach Maxwell (*44*) und Tantzen (*65*) werfen sie sich in Mäusejahren besonders auf die Feldmäuse. Verschiedene Möwen sind als Mäusefänger bekannt, namentlich in Mäusejahren; Maxwell (*44*) erwähnt neben "kleineren Möwen" die Mantelmöwe, Culemann (*78*) und Tantzen (*65*) die Silbermöwe, Tantzen (*65*) die Lachmöwe. Die Schleiereule ist durch Altum (*1*), Jaeckel (*34*), Geyr von Schweppenburg (*22*), Schneider (*57*), Guérin (*26*) und Uttendörfer (*72, 74*), die Waldohreule durch Altum (*2*), Jaeckel (*34*), Geyr von Schweppenburg (*22*), Greschick (*24, 25*), Rörig (*53*), Skovgaard (*63*), und Uttendörfer (*72*), die Sumpfeule durch Jaeckel (*34*), Rörig (*53*) Greschick (*25*) und Uttendörfer (*72*) als Mäusefängerin bekannt geworden. Der Steinkauz frisst nach Jaeckel (*34*), Geyr von Schweppenburg (*22*), Rörig (*53*), Greschick (*25*) und Uttendörfer (*72*) ziemlich viele Feldmäuse, sowie der Waldkauz, nach Altum (*1*), Jaeckel (*34*), Geyr von Schweppenburg (*22*), Rörig (*53*), Greschick (*25*) und Uttendörfer (*72*). Im Gegensatz zu den drei erstgenannten Eulen wird vermutlich der Steinkauz und nach Uttendörfer (*74*) sicher der Waldkauz von einer Feldmäusekalamität sehr wenig beeinflusst. H. Schenk (*55*) erwähnt im Mäusejahr 1930 den Raubwürger als Mäusevertilger. Krähen sind von mehreren Beobachtern als Mäusejäger, zumal und sehr tüchtig in Mäusejahren, angegeben worden: der Kolkrabe und die Rabenkrähe von Maxwell (*44*), die Nebelkrähe von Maxwell (*44*) und von Fernbach (*21*) und die Saatkrähe von H. Schenk (*56*), Béla Ratz (*5*), Gy. Matray (*43*) und Maxwell (*44*), während Tantzen (*65*) von "Krähen" ohne weiteres redet.

So haben die Feldmäuse eine unglaublich grosse Anzahl Raubfeinde. Trotzdem schwankt der Feldmausbestand regelmässig und kommen Plagen noch immer vor. Wie können wir uns das denken?

Zuerst gilt es festzustellen ob die Raubfeinde eine Abnahme der Feldmäuse bewirken. Wie unwahrscheinlich dieses klingt, doch ist es möglich, dass einer Art durch Raubfeinde nicht geschadet wird, weil durch den Einfluss der Raubfeinde Lücken in der Population entstehen, welche sofort von neuen Individuen ausgefüllt werden, welche sonst, unter Einfluss eines anderen "limiting factor," jedenfalls zu Grunde gegangen wären. Dieses ist nun bei Feldmäusen sicher nicht der Fall und die Raubfeinde drücken sicher die Konzentration. Man vergleiche für die Waldmaus auch Elton, Ford und Baker (*18*). Falls ihre Wirkung nun wirklich auf das Prinzip gegründet wäre: "nimm was du kriegen kannst," so könnten sie sogar die geringste Zunahme der Feldmäuse nie unterdrücken. Jedoch wohl abschwächen, denn die Dauer einer Periode zwischen zwei Maxima wird nicht von den Raub-

feinden, sondern vermutlich von anderen äusseren, über grosse Gebiete synchron verlaufenden Faktoren bedingt, und die Raubfeinde verlangsamen die Zunahme, drücken also den Bestand.

Nun ist aber: "Nimm was du kriegen kannst" nicht das einzige wichtige Prinzip. Wir haben es ausserdem noch mit zwei anderen Fähigkeiten der Raubfeinde zu tun: Migration und die Wahl einer günstigen Ernährungsstelle. Namentlich die Vögel können sich hierdurch sehr schnell in einem, von Feldmäusen übermässig dicht besiedelten Gebiet ansammeln, eben dadurch dass ein solches Gebiet eine zusagende Futterquelle bedeutet und dass sie dieses Gebiet durch Migration erreichen können. Obwohl jeder Vogel sich hier noch in derselben Weise ernährt und also der Feldmäusepopulation, den Populationen anderer Beutetiere gegenüber, nicht stärker als anders geschadet wird, bedeutet die Ansammlung der Raubfeinde im absoluten Sinn eine schwere Beeinträchtigung des Bestandes dieser Gegend. Wir sehen also, dass die migrierenden Raubfeinde sicher imstande sind, ein lokales Maximum zu unterdrücken.

Der quantitative Einfluss der Raubfeinde ist also wie folgt zu formulieren: Sie drücken fortwährend die Population der Feldmäuse. Lokale Maxima können völlig unterdrückt werden (Migration). Grössere und ausgedehntere Maxima entgehen sehr bald dem Einfluss der Raubfeinde. Ich kann mich hier am besten Geyr von Schweppenburg anschliessen, wenn er sagt: "Nur wenige Vögel halte ich für tatsächlich nützlich, und zu diesen gehören die Eulen. Sie sind meines Erachtens imstande, die Zahl der Mäuse in Schranken zu halten und in manchen Fällen Plagen vorzubeugen. Ist eine Kalamität allerdings einmal ausgebrochen, so können die Eulen nichts anderes tun, wie sich sattfressen, von einem Nutzen möchte ich dann nicht mehr reden." Etwas vorsichtiger, aber im Grunde vollkommen ähnlich drückt sich Middleton (45) aus: "Carnivorous enemies alone are totally inadequate to suppress any big plague. Small rodents possess such enormous powers of reproduction, that once they have passed a certain "critical point" in population only disease or food shortage can prevent their increase, while other conditions remain favourable. It is as a possible means of keeping the vole population below this critical point that carnivorous enemies are of economic value, and since the increase to a plague often takes place within the space of one breeding season, these enemies have little chance of keeping pace with it —although they certainly do their best."

Wir können also den quantitativen Einfluss der Raubfeinde auf die Bestandsschwankungen der Feldmäuse folgendermassen ausdrücken: die periodischen Schwankungen werden abgeschliffen. Dieses möge in ökonomischer Hinsicht wichtig sein (weil wir es hier mit der absoluten Bevölkerungsdichtigkeit zu tun haben), für eine tiefere Einsicht in die Ursachen der Bestandsschwankungen ist dem nur einen geringen Wert beizumessen.

Es sei aber sofort bemerkt, dass es möglicherweise auch noch einen qualitativen Einfluss gibt. Es braucht ja kein Zufall zu sein, dass gerade wenn die Feldmäuse der Kontrolle ihrer Raubfeinde, während einer Kalamität, entfliehen, eine Epidemie nach längerer oder kürzerer Zeit ausbricht. Wir müssen uns hier mit Ernst abfragen, ob im Verhältnis Raubvogel-Feldmaus von einer natürlichen Zuchtwahl, einem "survival of the fittest," die Rede sein kann. Es geht nicht an, hier schon à priori einen Standpunkt einzunehmen; wir müssen uns die Frage stellen, weil sie wichtig ist und weil es vielleicht nicht unmöglich ist sie zu beantworten.

Ich fasse noch einmal zusammen: der Einfluss der Raubfeinde auf den Feldmäusebestand ist quantitativ sehr wichtig, sie sind aber nicht imstande, einmal aufgetretene Kalamitäten stark zu beeinflussen. Die Frage nach den Ursachen der Feldmäuseschwankungen wird ihrer Lösung nur durch das Studium des Verhaltens und der Ökologie der Feldmäuse näher kommen.

C. DER EINFLUSS DER FELDMÄUSE AUF DAS LEBEN DER WALDOHREULE

Beim Sammeln der Gewölle machten wir selbstverständlich Beobachtungen an den Eulen selbst und dabei wurde uns schon bald klar, dass wir von dem Verhalten der Waldohreule noch nicht viel wissen. Es sei mir gestattet anlässlich der gemachten, allerdings gelegentlichen, Beobachtungen mit einigen Worten näher auf die Frage einzugehen, inwieweit die Nahrung seinen Einfluss gelten lässt auf das Verhalten der Waldohreule. Ist es doch in der Ökologie das Bestreben, die wechselseitigen Beziehungen der Tiere zu studieren.

Wie in den oben gegebenen Tabellen ersichtlich, sind die Feldmäuse die wichtigsten Beutetiere der Waldohreule. Fälle wo sie ganz fehlen sind äusserst selten, meistens nehmen sie über 50% der Beutetiere ein. Da wir nun wissen, dass die Individuenzahl der Feldmäuse so beträchtlichen Schwankungen unterlegen ist, so liegt es nahe zu fragen: (1) Inwieweit kann die Waldohreule ihren Bedarf in Zeiten starker Feldmausdepression mit anderen Beutetieren decken, oder zieht sie dann vielleicht nach besseren Gebieten? und (2) Welchen Einfluss haben die Feldmauskalamitäten auf das Brutgeschäft der Waldohreulen?

Ad (1). Zu dieser Frage gibt uns das merkwürdige Verhalten der Sumpfeule Veranlassung.

Die Sumpfeule ernährt sich in ungefähr derselben Weise wie die Waldohreule. Zwar sind Gewölluntersuchungen hier noch nie in dem Umfang wie bei der Waldohreule durchgeführt, aber die von Uttendörfer (72) referierten Angaben von Leisewitz (42), Greschick (25), Rörig (53) und Altum (1), die auf Gewöll- und Magenuntersuchungen stützen, zeigen dieses deutlich genug: 2 Wiesel, 20 Spitzmäuse, 1 Ratte, 278 Mus (Apodemus) spec., 1 Ziesel, 9 Evotomys glareolus, 1398 Microtus arvalis, 38 M. agrestis, 38 Vögel und 1 Frosch. Uttendörfer bemerkt hierzu: "so spricht alles dafür, dass die Sumpfohreule fast dieselbe Beute jagt, wie die Waldohreule. Nur scheint es so, als ob sie entsprechend ihrer etwas bedeutenderen Grösse . . . öfters auch etwas grössere Nager schlüge als jene."

In Zeiten grosser Feldmausplagen aber ernähren die Sumpfeulen sich fast ausschliesslich mit Feldmäusen. Sie sammeln sich dann in der Ruhezeit (im Gegensatz zu Brutzeit gemeint) zu Trupps an und verbleiben längere Zeit an günstigen Stellen. Wir können uns dieses wohl nicht anders vorstellen, als dass die Eulen auf dem Zuge durch besonders günstige Ernährungsbedingungen in ihrem Zugtrieb gehemmt werden.

Nicht nur zur Ruhezeit, sondern auch in der Brutzeit lassen sich die Sumpfeulen bei der Wahl ihres Aufenthaltsortes oft in auffallender Weise von den Ernährungsbedingungen leiten. In Mäusejahren brüten sie in ungewöhnlich grosser Anzahl in den von der Mäuseplage heimgesuchten Gegenden, selbst wenn sie dort sonst nicht brüten. Wir finden diesbezügliche Angaben bei Hudson (33) für Argentinien, bei Maxwell (44) für Schottland, und mehrere Beobachtungen in Ungarn (Kabáczy (35), Kiss (37), Cerva (78)). Wir können auch dieses unregelmässige Brüten wohl am besten durch eine Hemmung des Zugtriebes infolge günstiger Ernährungsbedingungen verstehen.

Es ist nach dem Vorhergehenden ohne Weiteres klar, dass der Zug der Sumpfeule von dem Vorhandensein guter Feldmausgebiete beeinflusst wird. Und obwohl die Feldmäusekalamitäten eine über grosse Gebiete synchron verlaufende Periodizität aufweisen, sind doch immer auch in Feldmäuseminima noch viele gute Feldmausgebiete vorhanden. Durch dieses Verhalten der Eulen wird somit erreicht, dass der Feldmausgehalt ihrer Nahrung höher ist, als er es bei residenten Eulen sein würde.

Es fragt sich nun, inwieweit die Waldohreule, die der Sumpfeule sowohl ernährungsökologisch wie systematisch so nah steht, ein ähnliches Verhalten zeigt.

Ansammlungen von Waldohreulen in der Ruhezeit in von einer Feldmäuseplage heimgesuchten Gegenden sind öfters beobachtet worden (z. B. Dobbrick (12) Uttendörfer (72)). In anderen Fällen ist es nicht sicher, ob eine Ansammlung von Mäuseüberfluss bedingt wurde (z. B. Schuster (59), Poll (50)).

Unsere Beobachtungen in verschiedenen Waldohreulengebieten zeigen nun in dieser Hinsicht noch manches Interessante. Es sei zuvor bemerkt, dass sie sich erst über 1½-2 Jahre erstrecken und dass sie also noch sehr fragmentarisch sind.

Bei Betrachtung der Tabellen 5-10 wird dem Leser aufgefallen sein, dass die Waldohreule sich bei niedriger Feldmäusekonzentration oft fast ganz von anderen Tieren ernähren kann. Es ist ihr in bestimmten Gebieten möglich sich ohne die Feldmäuse zu helfen. Anscheinend ist das in vielen anderen Gegenden nicht der Fall. Wenn wir die Waldohreulenbesiedelung in unserer Umgebung im Winter 1931-'32 und im Winter 1930-'31 vergleichend betrachten, so fällt auf, dass in dem feldmäusereichen Winter 1930-'31 mehr Ruheplätze besetzt waren als im Winter 1931-'32. Tabelle 17 und Tabelle 19 zeigen ein Gebiet, dass im Winter 1930-'31 besser besiedelt war als im nachfolgenden Winter. Die in dem Winter 1931-'32 gesammelten Gewölle fanden sich nur gelegentlich und in sehr kleinen Mengen, hauptsächlich in

der Herbst- und Frühjahrsdurchzugzeit. Dagegen stellt sich heraus, dass in den von anderen Beutetieren dichter besiedelten Gebieten im Winter 1931-'32 im Allgemeinen mehr Waldohreulen überwintert haben als im vergangenen Winter, was aus den Zahlen der geschlagenen Beutetiere ohne Weiteres ersichtlich ist. Hier muss bemerkt werden, dass die Eulen vermutlich bei Feldmäuseüberfluss mehr Feldmäuse fressen als sie brauchen, sodass die für den Winter 1930-'31 gefundenen Beutetierzahlen relativ zu hoch erscheinen.

In dem "Feldmäusewinter" 1930-'31 überwinterten die Eulen aller Anschein nach also mehr zerstreut, und im Winter 1931-'32 blieben vor allem diejenigen Gebiete leer, die auch im feldmäusereichen Winter die wenigsten Eulen ernähren konnten. In diesem Winter zogen die Eulen sich auf diejenigen Gebiete zusammen, die auch im vorhergegangenen Winter die meisten Eulen beherbergt hatten.

Diese an der holländischen Küste überwinternden Eulen sind vermutlich zum grössten Teil fremde Vögel. Unsere Brutvögel scheinen schon wegzuziehen, lange bevor sich die Überwinterer einstellen. Weil diese Verhältnisse, wie es mir scheint, noch nicht bekannt sind, gebe ich meine Beobachtungen ziemlich ausführlich.

(1) Von einer Stelle (Tabelle 18) holten wir uns Ende März 1931 ca 3000 Gewölle, die anscheinend von einer ganzen Gesellschaft herrührten. In diesem Gebiet waren den ganzen Sommer 1931 hindurch eine oder zwei Eulen; es war uns nicht möglich festzustellen ob sie brüteten oder nicht. Ende Juli oder im Laufe des Monats August aber sind diese Eulen verschwunden. Dieses ist an dem Ausbleiben der Gewölle und der Mauserfedern sehr leicht festzustellen. Erst Ende Oktober trafen wieder 2 Eulen ein, und Mitte November waren plötzlich 15 Stück da. Bis Mitte Dezember war keine Änderung festzustellen, am 19. Dezember waren aber 30 Eulen an der Stelle. Diese blieben nicht alle, und bald war ihre Zahl wieder auf ca 15 zurückgegangen. Bis Mitte März sind dann ungefähr 10 Stück geblieben.

Wir haben uns oft gefragt, weshalb es eben in diesem kleinen Gebiet so viele Waldohreulen gibt. Der Grund dazu ist vielleicht in zwei verschiedenen Umständen zu suchen. Erstens ist in den angrenzenden flachen Dünenwiesen eine sehr niedrige Vegetation. Eine hohe Vegetation macht es den Raubfeinden der Feldmäuse beträchtlich schwieriger ihr nahe zu kommen. Das beweisen die Beobachtungen Kramer's (39) für einige Sperberpaare, die nach der Ernte, als die Feldmäuse nicht mehr zwischen dem hohen Gras usw. lebten, plötzlich viel mehr Feldmäuse schlugen als vorhin. Für die Waldohreule berichtete ich an anderer Stelle (68) über einen ähnlichen Fall, wobei der Prozentsatz der in den Gewöllen enthaltenen Feldmäuse von ca 50% bis zu ca 90% stieg. Zweitens findet, wie die Jagdaufseher uns versicherten, und wie wir es auch an den jagenden Turmfalken beobachten können, in nassen Zeiten eine Umsiedlung der Feldmäuse statt; sie ziehen aus den Polderwiesen nach den höheren und durchlässigeren Dünenwiesen. Im Winter wird also das Dünengebiet dichter von Feldmäusen bevölkert sein als der Polder. Und da Waldmäuse und Singvögel häufig sind, ist die Nahrungsmenge für die Eulen beträchtlich.

(2) In einem ca 1000 M. vom vorigen Terrain entfernten Stück Stangenholz brütete im Sommer 1931 ein Paar Waldohreulen. Die Jungen wurden noch Ende Juni gehört; als wir Anfang September das Wäldchen besuchten, waren die Eulen verschwunden und aus dem Mangel an Mauserfedern liess sich schliessen, dass sie schon längere Zeit fort waren. Erst Mitte November 1931 siedelten sich plötzlich wieder 5 Eulen an, die aber bald wieder verschwanden.

(3) Ende November 1931 erhielten wir auf unsere Nachfrage ca 400 Gewölle, die in einem kleinen Stück Stangenholz in den Dünen Texels gefunden worden waren. Es hielt sich da ein Waldohreulentrupp auf, und da sämtliche Gewölle auffällig frisch, und ausserdem keine Mauserfedern vorhanden waren, haben wir Grund anzunehmen, dass auch diese Eulen Anfang oder Mitte November angekommen waren.

(4) Im Süden Texels haben sich Ende Oktober 1931 nach Mitteilung des Herrn Kikkert mindestens 5 Waldohreulen eingestellt. Als ich Anfang Januar zur Stelle war konnte ich ca 20 Eulen beobachten. Diese Eulen oder wenigstens der grösste Teil, sind bis Mitte März geblieben.

(5) In der Nähe von Velsen (bei Tymuiden) waren am 21 November 1931 15 Eulen anwesend, sie blieben den ganzen Winter; Mitte März waren noch 8 Stück da.

(6) Ende Januar trafen in einem Dünenwäldchen beim Haag 11 Eulen ein, die hier bis Ende März blieben. Hier brüten keine Eulen, vielleicht manchmal ein Paar.

(7) Mitte Februar fielen in ein anderes Stück Stangenholz beim Haag 7 Eulen ein, die erst Anfang April verschwanden. In diesem Gebiet brütet regelmässig ein, möglich zwei Paare.

(8) Ähnliche überwinternde Waldohreulentrupps, von denen ich die genaue Ankunftzeit nicht weiss, aber deren Gewöllezahl, im Vergeich mit der Anzahl der beobachteten Eulen, angibt, dass sie erst im Herbst angekommen sein können, sind mir noch bekannt geworden von: Ameland (den 9. März 10 bis 15 Eulen), Haarlem (den 27. März 5 Eulen), Walcheren (mehrere Trupps von einigen bis zu 10 Stück) und Rotterdam (an zwei Stellen je einige, während kurzer Zeit im Dezember je 7 Stück).

Es ergibt sich aus diesen Beobachtungen noch die ökologisch interessante Tatsache, dass unsere Dünen im Winter erheblich dichter von Waldohreulen besiedelt sind als im Sommer, obwohl doch im Sommer im allgemeinen mehr Mäuse, Feldmäuse und auch Vögel vorhanden sind. Zwar braucht ein Brutpaar für 5 oder 6 Eulen Nahrung, aber die Anzahl der Beutetiere steigt auch ungefähr in diesem Masse, die der Mäuse sogar viel schneller.

Ad (2) Bei der Schleiereule und bei der Sumpfeule sehen wir noch eine andere Reaktion auf das Vorhandensein vieler Feldmäuse. Die während 32 Jahre fortgeführten Beobachtungen B. und W. Schneider's (57) an der

Schleiereule zeigen, dass diese Eule in Feldmäusejahren zweimal brütet und in Jahren, die besonders arm an Feldmäusen sind, manchmal gar nicht brütet. Die erste Brut fiel jedesmal in die normale Brutzeit, die Jungen der zweiten Brut flogen dann erst im Winter, einmal erst im Anfang des Januar, aus. Ausserdem war die Eizahl der zweiten Brut meistens grösser als normal, vielleicht entsprechend der grösseren Feldmäusezahl am Ende des Sommers. Schon Jaeckel (34), der in zeiner "Systematischen Übersicht der Vögel Bayerns" so viele sorgfältige Feldbeobachtungen an vielen Vögeln mitteilt, gibt vieles Interessante über das Verhalten der Schleiereule in Mäusejahren, die mit den Angaben der Schneider's im Einklang sind.

Jaeckel gibt auch an, dass von verschiedenen Raubvögeln Nester mit ausserordentlich grossen Eiern während Mäuseplagen gefunden wurden.

Andere Beobachtungen über zweimaliges Brüten in Mäusejahren und über grössere Bruten als normal findet man bei Kleinschmidt (38), Uttendörfer (74) und Guérin (26), und verschiedene Handbücher erwähnen das zweimalige Brüten der Schleiereule (vgl. Vasvári (77)).

Noch auffälliger ist das Verhalten der Sumpfeule. An verschiedenen Stellen finden wir das zweimalige Brüten und das Zeitigen besonders grosser Bruten während Feldmauskalamitäten erwähnt (vgl. Maxwell (44), H. Schenk (54), Kabáczy (35), Hudson (33), Bailey (3), Hewitt (31), Barret Hamilton and Hinton (4), Collet (10), Bengt Berg (6)).

Sehen wir die diesbezügliche Literatur über die Waldohreule durch, so findet sich hier recht wenig. Es scheint, dass hier zweimaliges Brüten sehr selten vorkommt, jedenfalls ist es sehr selten beobachtet worden. Ich kenne aus der Literatur bloss zwei Angaben. Csörgey (11) beschreibt zweimaliges Brüten zweier Waldohreulenpaare im Sommer 1907 (?) in Ungarn; die unter den Horstbäumen gefundenen Gewölle enthielten ausschliesslich "Mäuse." Die andere Angabe (Robien (52)) erwähnt jedoch keine Beziehung zu einem Mäusejahr, ist ausserdem ein wenig zweifelhaft.

Es fragt sich nun, wodurch die Waldohreule hier so anders reagiert als die Sumpfeule und die Schleiereule. In einer vorigen Mitteilung (68) beschrieb ich, wie die Jungen einer von mir beobachteten Brut während voller zwei Monate nach dem Flüggewerden vollständig von den Alten mit Nahrung versorgt wurden. Ich äusserte damals die Vermutung, dass ein solches Verhalten mit der Unfähigkeit, eine doppelte Brut zu erziehen, zusammenhängen könnte. Es gibt aber verschiedene Tatsachen, die uns hier zu grösster Vorsicht mahnen. In dem von Csörgey erwähnten Fall "schritten die beiden Eulenpaare nach dem Flüggewerden der je 4 Jungen sofort zur neuen Brut." Ausserdem werden z.B. junge Schleiereulen und vielleicht junge Sumpfeulen auch ziemlich lange von den Eltern ernährt. Ich kenne keine ausschlaggebenden Beobachtungen hierüber in der Literatur; die Angaben Heinroth's in "Die Vögel Mitteleuropas" (28) reichen hierzu auch nicht aus. Schliess-

lich kenne ich eine Beobachtung meines Freundes Jan P. Strijbos, der gesehen hat, dass Kormorane die Jungen ihrer ersten Brut noch fütterten, als sie schon aufs neue Junge hatten. Diese Umstände würden zu der Vermutung nötigen, dass es einen physiologischen Grund für das abweichende Verhalten der Waldohreule gäbe.

Wir müssen hier also manche Frage noch ganz offen lassen. Genaue Durchbeobachtung einiger Bruten mit Berücksichtigung der Umweltsverhältnisse wird uns vielleicht schon einige Auskunft geben können. Meine diesbezüglichen Bemühungen sind auch dieses Jahr leider durch Zerstörung eines besonders günstigen Horstes misslungen.

IX. ZUSAMMENFASSUNG DER ERGEBNISSE

Das Studium der Gewölle der Waldohreule (*Asio o. otus* L.) gibt uns genaue Angaben über die Ernährung dieser Eule. Die Feststellungen wurden an einem sich über ca 23000 Beutetiere erstreckenden Material gemacht. Die zeitlichen und örtlichen Schwankungen in der Zusammenstellung der Nahrung verlaufen in Übereinstimmung mit den Schwankungen in der Zusammenstellung des erreichbaren Nahrungsvorrats. Sie sind also immer von der Zusammenstellung der Umgebung bedingt. Hieraus lässt sich schliessen, dass die Eulen nehmen, was ihnen auf ihren Jagdzügen begegnet, und dass "Spezialisten" im Sinne Uttendörfer's, die eine individuelle Bevorzugung bestimmter Beutetiere geltend machen, unter den Waldohreulen nicht vorkommen. Dieses gilt nur für gröbere, ökologisch wichtige Schwankungen, über ökologisch zu vernachlässigende, aber psychologisch vielleicht noch wichtige, kleinere Unterschiede ist auf Grund der Feldbeobachtungen nichts zu sagen. Ein ähnliches Prinzip scheint auch der Ernährungsökologie mancher anderer Eulen und Raubvögel zu Grunde zu liegen; am überzeugendsten ist dieses wohl beim Sperber dargetan worden.

Um die wechselseitigen Beziehungen zwischen der Waldohreule und der Feldmaus näher zu betrachten, werden zuerst die periodischen Bestandsschwankungen, mit deren Studium man sich in England unter der Führung Elton's beschäftigt, kurz behandelt. Die Ursachen dieser Schwankungen liegen vermutlich in noch nicht klaren, klimatischen Perioden; die Kontrolle durch Raubfeinde erwies sich als äusserst wichtig, namentlich solange die Population der Mäuse unter einer bestimmten Schwelle bleibt; gelangt sie infolge sehr günstiger klimatischer Verhältnisse über diese Schwelle hinaus, so können die Raubfeinde einer "Plage" unmöglich mehr vorbeugen.

Das Leben der Waldohreule wird von den Feldmäusen in verschiedener Weise beeinträchtigt, jedoch in auffallend geringerem Ausmass als das Leben der ernährungsökologisch sowie systematisch so nah verwandten Sumpfeule und Schleiereule. Die holländischen Waldohreulen ziehen vermutlich im Nachsommer weg; erst spät im Herbst, Ende Oktober und November, treffen

plötzlich sehr viele Waldohreulen ein, die in Trupps bis zu 15, gelegentlich bis zu 30 Stück, überwintern. Im feldmäusereichen Winter 1930-'31 überwinterten die Eulen mehr zerstreut als im feldmausärmeren Winter 1931-'32; im zweiten Winter zogen sich die Eulen auf diejenigen Gebiete zusammen, die auch im vorigen Winter die meisten Eulen herbergten, und die ausserdem einen besonders hohen Bestand anderer Beutetiere aufwiesen. In diesen Gebieten überwinterten mehr Eulen als im vorigen Winter, in die kleineren Gebiete, die nur während Feldmäusemaxima überhaupt bewohnbar schienen, kamen im zweiten Winter nur gelegentlich Eulen. Auch was die bei Sumpfeule und Schleiereule so besonders stark ausgeprägte Beeinflussung des Brutgeschäfts betrifft, weicht die Waldohreule in auffälliger Weise ab; zweimaliges Brüten kommt sehr selten vor, und Vergrösserung der Eizahl ist m.W. nicht beobachtet worden. Die Ursachen dieses abweichenden Verhaltens wären in physiologischen Unterschieden zu suchen.

X. LITERATURVERZEICHNIS[3]

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TABELLE 1. *Übersicht unserer Ergebnisse.**

Fledermaus (*Chiropteron*)	4
Maulwurf (*Talpa europaea europaea* L.)	5
Spitzmaus (*Sorex* sp.)	215
Wasserspitzmaus (*Neomys fodiens fodiens* (Schreb.))	5
Hausspitzmaus (*Crocidura russula russula* (Herm.))	4
Feldmaus (*Microtus arvalis fulvus* (Geoffr.))	10280
Rattenkopf (*Microtus ratticeps arenicola* De Sél. L.)	2094
Wasserratte (*Arvicola terrestris scherman* (Shaw))	37
Waldwühlmaus (*Clethrionomys glareolus glareolus* (Schreb.))	224
Waldmaus (*Apodemus sylvaticus sylvaticus* (L.))	7396
Zwergmaus (*Micromys minutus soricinus* (Herm.))	12
Wanderratte (*Rattus norvegicus norvegicus* (Erxl.))	224
Hausmaus (*Mus musculus musculus* L.)	180
Eichhörnchen (*Sciurus vulgaris russus* Miller)	1
Kaninchen (*Oryctolagus cuniculus fodiens* (Gray))	9
Vögel	3279
Frösche (*Rana temporaria* L.)	1
Fische	1
Insekten	61

TABELLE 2. *Die Angaben über die Ernährung deutscher Waldohreulen (nach Uttendörfer, Altum, Faeckel, Rörig, Geyr von Schweppenburg).***

Fledermaus (*Chiropteron*)	4
Wiesel (*Mustela nivalis nivalis* L.)	2
Maulwurf (*Talpa europaea* L.)	33
Wasserspitzmaus (*Neomys fodiens fodiens* (Schreber))	2
Spitzmaus (*Sorex araneus araneus* (L.))	106
Hausspitzmaus (*Crocidura russula russula* (Hermann))	13
Siebenschläfer (*Glis glis glis* (L.))	1
Maus (*Mus, Apodemus, Micromys*)	2399
Kleine Haselmaus (*Muscardinus avellanarius* (L.))	1
Hamster (*Cricetus cricetus cricetus* (L.))	3
Wasserratte (*Arvicola scherman* (Shaw))	22
Waldwühlmaus (*Clethryonomys glareolus glareolus* (Schreber))	198
Gemeine Feldmaus (*Microtus arvalis* (Pall.))	15947
Rattenkopf (*Microtus ratticeps* (Keyserling und Blasius))	3

* Die subspezifische Benennung der Beutetiere ist im Anschluss an den faunistischen Übersichten von Van Den Brink (7), (Säugetiere) und Van Oordt und Verwey (49), (Vögel).

Die Vögel verteilen sich wie folgt über die folgenden Arten: 1 Fasan (*Phasianus colchicus* L.), 1 Wasserralle (*Rallus aquaticus aquaticus* L.), 10 Wacholderdrosseln (*Turdus pilaris* L.), 1 Misteldrossel (*Turdus viscivorus viscivorus* L.), 7 Weindrosseln (*Turdus musicus* L.), 6 Amseln (*Turdus merula merula* L.), 149 Drosseln spec. (wohl meist *merula*), 4 Steinschmätzer (*Oenanthe oenanthe* L.), 35 Rotkehlchen (*Erithacus rubecula* (L.)), 3 Zaunkönige (*Troglodytes troglodytes troglodytes* (L.)), 1 Grauer Fliegenschnäpper (*Muscicapa striata striata* (PALL.)), 29 Feldlerchen (*Alauda arvensis arvensis* L.), 50 Kohlmeisen (*Parus major major* L.), 15 Blaumeisen (*Parus coeruleus coeruleus* L.), 1 Tannenmeise (*Parus ater ater* L.), 2 Schwanzmeisen (*Aegithalos caudatus europaeus* (Herm.)), 1 Gartenbaumläufer (*Certhia brachydactyla brachydactyla* Brehm), 5 Goldhähnchen (*Regula* spec.), 56 Stare (*Sturnus vulgaris vulgaris* L.), 616 Finken (*Fringilla* spec., *coelebs* oder *montifringilla*), 61 Zeisige (*Carduelis spinus* (L.), 43 Bluthänflinge (*Carduelis cannabina cannabina* (L.)), 1516 Hausspatzen (*Passer domesticus domesticus* (L.)), 149 Feldsperlinge (*Passer montanus montanus* (L.)), 2 Kreuzschnäbel (*Loxia curvirostra curvirostra* L.), 96 Grünlinge (*Chloris chloris chloris* (L.)), 3 Goldammern (*Emberiza citrinella citrinella* L.), 223 Pfriemenschnäbler spec., 99 Kegelschnäbler spec. und 91 Vögel spec.

Die Insekten gehören den folgenden Arten zu: 30 *Geotrupes* spec., 21 *Dytiscus* spec., 3 *Hydrophilus piceus* L., 4 *Larven von Dytiscus oder Hydrophilus*, 3 *Polyphylla fullo* L.

** Die subspezifische Bennenung nach Brohmer (8).

Erdmaus (*Microtus agrestis* (L.))	295
Hase, Kaninchen (*Lepus oder Oryctolagus*)	10
Vögel	279
Frösche	46
Fische	1
Insekten	manche

TABELLE 3. *Die Nahrung ungarischer Waldohreulen (nach Greschick (24, 25))*

Spitzmaus (*Sorex* sp.)	2
Waldmaus (*Apodemus sylvaticus* (L.))	226
Brandmaus (*Apodemus agrarius* (Pall.))	5
Hausmaus (*Mus musculus musculus* L.)	45
Zwergmaus (*Micromys minutus soricinus* (Herm.))	1
Kleine Haselmaus (*Muscardinus avellanarius* (L.))	1
Muride spec.	7
Wasserratte (*Arvicola scherman* (Shaw))	1
Gemeine Feldmaus (*Microtus arvalis* (Pall.))	899
Rattenkopf (*Microtus ratticeps* Keys. und Blasius)	3
Hase (*Lepus europaeus* Pall.)	1
Vögel	56
Käfer	13

TABELLE 4. *Die Nahrung dänischer Waldohreulen (nach Skovgaard (63)).*

Maulwurf (*Talpa europaea* L.)	3
Spitzmaus (*Sorex araneus* (L.))	215
Zwergspitzmaus (*Sorex minutus* L.)	174
Wasserspitzmaus (*Neomys fodiens* (Schreber))	5
Waldwühlmaus (*Clethrionomys glarcolus* (Schreber))	65
Wasserratte (*Arvicola scherman* (Shaw))	33
Gemeine Feldmaus (*Microtus arvalis* (Pallas))	2461
Erdmaus (*Microtus agrestis* (L.))	1942
Wanderratte (*Epimys norvegicus* (Erxl.))	8
Hausmaus (*Mus musculus musculus* L.)	271
Zwergmaus (*Micromys minutus* (Pall.))	211
Waldmaus (*Apodemus sylvaticus* (L.))	3211
Vögel	821
Insekten	manche

Die Vögel verteilen sich über die folgenden Arten: 2 Tringen oder Totanus, 1 Bekassine (*Capella gallinago* (L.)), 55 Schwalben (*Hirund* sp.), 7 Wacholderdrosseln (*Turdus pilaris* L.), 7 Amseln (*T. merula* (L.)), 7 Drosseln (*Turdus* sp.), 2 Rotschwänze (*Phoenicurus phoenicurus* (L.)), 1 Rotkehlchen, (*Erithacus rubecula* (L.)), 2 Mönchsgrasmücken (*Sylvia atricapilla* L.), 1 Gartenspötter (*Hippolais icterina* (Viell.)), 2 Fitislaubsänger (*Phylloscopus trochilus* L.), 1 Laubsänger (*Phylloscopus* spec.), 8 graue Fliegenschnäpper (*Muscicapa striata* (Pall.), 3 Trauerfliegenschnäpper (*Muscicapa hypoleuca* (Pall.)), 65 Lerchen (*Alauda*, sp., nach schriftlicher mitteilung des Herrn Skovgaard wohl arvensis L.), 7 Wiesenpieper (*Anthus pratensis* (L.)), 9 Pieper (*Anthus* spec.), 5 Kohlmeisen (*Parus major* L.), 7 Meisen (*Parus* sp.), 35 Goldhähnchen (*Regulus* sp.), 5 Stare (*Sturnus vulgaris* L.), 48 Buchfinken (*Fringilla coelebs* L.), 2 Erlenzeisige (*Carduelis spinus* (L.)), 71 Bluthänflinge (*Carduelis cannabina* (L.), 168 Hausspatzen (*Passer domesticus* (L.)), 9 Feldsperlinge (*Passer montanus* (L.)), 24 Grünlinge (*Chloris chloris* (L.)), 18 Grauammern (*Emberiza calandra* L.), 49 Goldammern (*E. citrinella* L.), 3 Ammern spec. (Emberiza spec.), 54 Pfriemenschnäbler spec. und 143 Vögel spec.

TABELLE 5. *Die Nahrung der texelschen Waldohreulen im Winter 1931-'32.*

Wasserspitzmaus	5	Rattenkopf	2092
Crocidura	1	Kaninchen	3
Hausmaus	23	Vögel	145
Waldmaus	1722	Insekten	17
Wanderratte	47		

TABELLE 6. *Die Nahrung der ameländer Waldohreulen im Winter 1931-'32.*

Waldspitzmaus	1	Kaninchen	2
Hausmaus	18	Vögel	31
Waldmaus	2956	Frosch	1
Gemeine Feldmaus	44	Geotrupes	4

TABELLE 7. *Die Nahrung der Waldohreulen eines Dünenwäldchens unweit Haarlems im Winter 1931-'32.*

Waldspitzmaus	80	Gemeine Feldmaus	173
Hausmaus	1	Waldwühlmaus	20
Zwergmaus	4	Kaninchen	1
Waldmaus	154	Vögel	29
Wanderratte	1	Insekten	2

TABELLE 8. *Die Nahrung der Rotterdamer Stadteulen im Winter 1931-'32.*

Hausmaus	1	Feldsperling	4
Waldmaus	11	Fink	9
Gemeine Feldmaus	32	Grünling	1
Haussperling	161	Star	1

TABELLE 9. *Die Nahrung einiger walcherschen Waldohreulen im Winter 1931-'32.*

Fledermaus	1	Bluthänfling	1
Crocidura	3	Grünling	2
Hausmaus	1	Goldammer	1
Waldmaus	15	Star	6
Wanderratte	1	Kohlmeise	1
Wasserratte	1	Drossel	17
Gemeine Feldmaus	7	Rotkehlchen	3
Haussperling	41	Pfriemenschnäbler spec.	11
Feldsperling	2	Dytiscus	1
Fink	18		

TABELLE 10. *Die Nahrung der Waldohreulen eines und desselben Gebietes in zwei verschiedenen Perioden.*

	Winter 1930-'31	Winter 1931-'32
Fledermaus	1	1
Waldspitzmaus	12	57
Hausmaus	229	29
Waldmaus		337
Wanderratte	18	49
Wasserratte	4	6
Gemeine Feldmaus	3497	1339
Waldwühlmaus	44	54
Hausspatz	51	279
Fink	42	235
Andere Vögel	68	186
Insekten	7	5

TABELLE 11. *Die Nahrung einer Waldohreulenbrut bei Harderwijk, im Sommer 1931.*

Maulwurf	5	Wasserratte	10
Waldspitzmaus	15	Feldmaus	122
Waldmaus	26	Waldwühlmaus	10
Wanderratte	1	Vögel	32

TABELLE 12. *Die Nahrung der in der unmittelbaren Nähe vom Haag verbleibenden Eulen im Winter 1931-'32.*

Waldspitzmaus	4	Waldwühlmaus	11
Hausmaus	34	Kaninchen	2
Zwergmaus	1	Haussperling	318
Waldmaus	167	Fink	52
Wanderratte	15	Zeisig	29
Wasserratte	4	Andere Vögel	113
Gemeine Feldmaus	340	Insekten	2

TABELLE 13. *Ein Vergleich zwischen dem Sperling- bezw. Zeisiggehalt der Sperber- und Waldohreulennahrung im "Spatzengebiet" mit dem Durchschnittswert für beide Arten. Zwischen Klammern stehen jedesmal die Zahlen der im ganzen nachgewiesenen Vögel, kursiv der Prozentsatz.**

	"Spatzen- und Zeisiggebiet"	Im Durchschnitt
Sperling von Waldohreule	318 (510) *62%*	1516 (3279) *46%*
Sperling von Sperber	18 (92) *20%*	61 (832) *7%*
Zeisig von Waldohreule	29 (510) *6%*	49 (3279) *1,5%*
Zeisiz von Sperber	4 (92) *4%*	9 (832) *1%*

* Die Prozentzahlen sind bloss zum Vergleich gegeben; das Berechnen einer mittleren Fehler ist natürlich unmöglich. *Inwieweit* diesen Zahlen denn auch Wert beizumessen ist, muss ein jeder für sich ausmachen.

TABELLE 14. *Der Finkengehalt der Nahrung von Sperbern und Waldohreulen im "Finkengebiet," im Vergleich mit dem Durchschnittswert der von beiden Arten erbeuteten Finken.*

	"Finkengebiet"	Im Durchschnitt
Fink von Waldohreule	*277* (861) *32%*	616 (3279) *19%*
Fink vom Sperber	*32* (85) *38%*	176 (832) *21%*

TABELLE 15. *Die Nahrung der Waldohreulen eines holländischen Dünengebietes in vier verschiedenen Perioden, die Bestandsschwankungen der Feldmäuse zeigend.*

Feldmaus	45 = *42%*	
Waldmaus	*22* = *21%*	
Andere Säugetiere	4 = *4%*	
Hausspatz	*20* = *19%*	
Andere Vögel	15 = *14%*	Sommer 1930
Feldmaus	530 = *90%*	
Waldmaus	20 = *4%*	
Andere Säugetiere	8 = *1,5%*	
Hausspatz	14 = *2%*	
Andere Vögel	15 = *2,5%*	Winter 1930-1931
Feldmaus	90 = *70%*	
Waldmaus	18 = *14%*	
Andere Säugetiere	5 = *4%*	
Hausspatz	4 = *3%*	
Andere Vögel	11 = *9%*	Sommer 1931
Feldmaus	168 = *61%*	
Waldmaus	57 = *21%*	
Andere Säugetiere	13 = *5%*	
Hausspatz	11 = *4%*	
Andere Vögel	*24* = *9%*	Winter 1931-1932

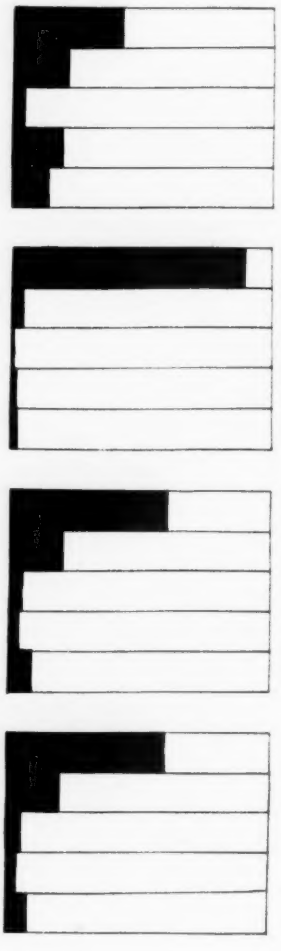


TABELLE 16. *Die Nahrung der Waldohreulen eines 2. Gebietes in vier verschiedenen Perioden, die Bestandsschwankungen der Feldmäuse in ähnlicher Weise zeigend.*

Feldmaus	84 =	*30%*
Waldmaus	104 =	*37%*
Andere Säugetiere	14 =	*5%*
Haussperling	47 =	*17%*
Andere Vögel	28 =	*11%*
Feldmaus	147 =	*68%*
Waldmaus	37 =	*17%*
Andere Säugetiere	11 =	*5%*
Hausspatz	3 =	*1,5%*
Andere Vögel	18 =	*8%*
Feldmaus	154 =	*53%*
Waldmaus	39 =	*13%*
Andere Säugetiere	6 =	*2%*
Hausspatz	47 =	*16%*
Andere Vögel	43 =	*16%*
Feldmaus	321 =	*38%*
Waldmaus	221 =	*26%*
Andere Säugetiere	97 =	*11%*
Hausspatz	81 =	*10%*
Andere Vögel	128 =	*15%*

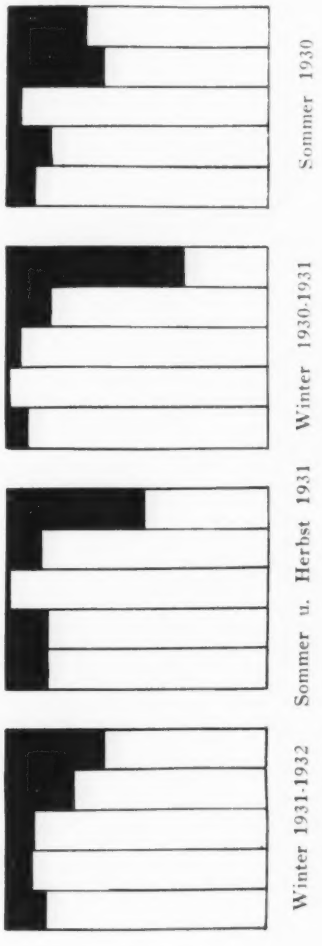


TABELLE 17. *Die Nahrung der Waldohreulen eines 3. Gebietes in drei verschiedenen Perioden (Die Kontrolle erst im Winter 1930-'31 angefangen).*

Feldmaus	399 = 90%	
Waldmaus	20 = 5%	
Andere Säugetiere	4 = 1%	
Hausspatz	4 = 1%	
Andere Vögel	12 = 3%	Winter 1930-1931
Feldmaus	103 = 50%	
Waldmaus	43 = 21%	
Andere Säugetiere	23 = 11%	
Hausspatz	25 = 12%	
Andere Vögel	11 = 6%	Sommer u. Herbst 1931
Feldmaus	30 = 31%	
Waldmaus	27 = 28%	
Andere Säugetiere	16 = 17%	
Hausspatz	2 = 2%	
Andere Vögel	12 = 12%	Winter 1931-1932

TABELLE 18. *Die Nahrung der Waldohreulen eines 4. Gebietes in drei verschiedenen Perioden (Die Kontrolle erst im Winter 1931-'32 angefangen).*

Feldmaus	3052 = 89%	
Waldmaus	198 = 6%	
Andere Säugetiere	61 = 2%	
Hausspatz	37 = 1%	
Andere Vögel	94 = 3%	Winter 1930-1931
Feldmaus	296 = 87%	
Waldmaus	6 = 1,5%	
Andere Säugetiere	6 = 1,5%	
Hausspatz	17 = 5%	
Andere Vögel	13 = 4%	Sommer 1931
Feldmaus	1339 = 52%	
Waldmaus	337 = 13%	
Andere Säugetiere	196 = 8%	
Hausspatz	279 = 11%	
Andere Vögel	426 = 16%	Winter 1931-1932

TABELLE 19. *Die Nahrung der Waldohreulen eines 5. Gebietes, in zwei nachfolgenden Wintern (Im Sommer keine Eulen angetroffen).*

	Winter 1930-1931	Winter 1931-1932
Feldmaus	728 = *86%*	330 = *30%*
Waldmaus	57 = *7%*	163 = *15%*
Andere Säugetiere	17 = *2%*	70 = *7%*
Hausspatz	22 = *2%*	323 = *30%*
Andere Vögel	25 = *3%*	191 = *18%*

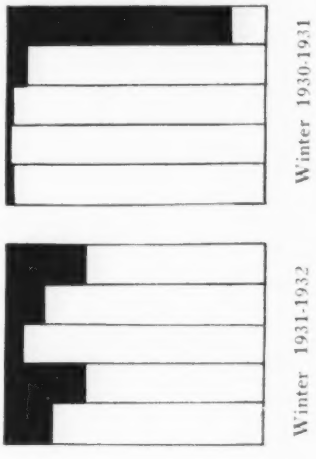


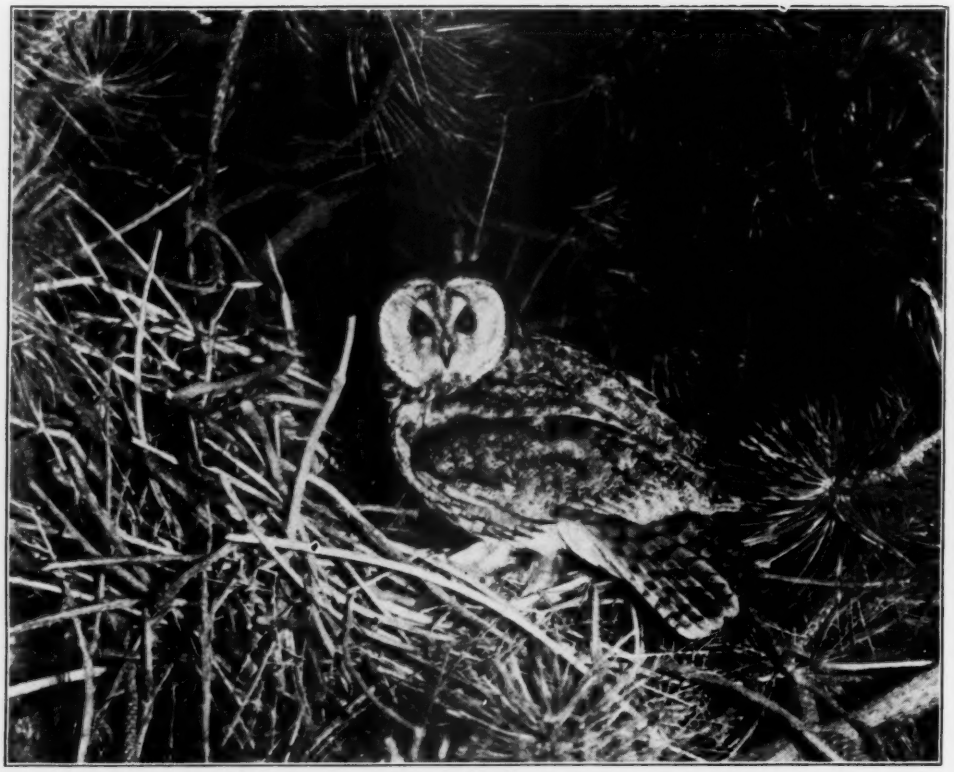
TABELLE 20. *Die Nahrung einer Waldohreulenbrut im Sommer 1931, den Einfluss der Ernte zeigend.*

	Vor der Ernte	Nach der Ernte
Maulwurf	5 = *3%*	—
Spitzmaus	15 = *8%*	—
Waldmaus	23 = *12%*	3 = *9%*
Wanderratte	1	—
Wasserratte	10 = *5%*	—
Gemeine Feldmaus	92 = *49%*	30 = *88%*
Waldwühlmaus	10 = *5%*	—
Vögel	31 = *17%*	1 = *3%*

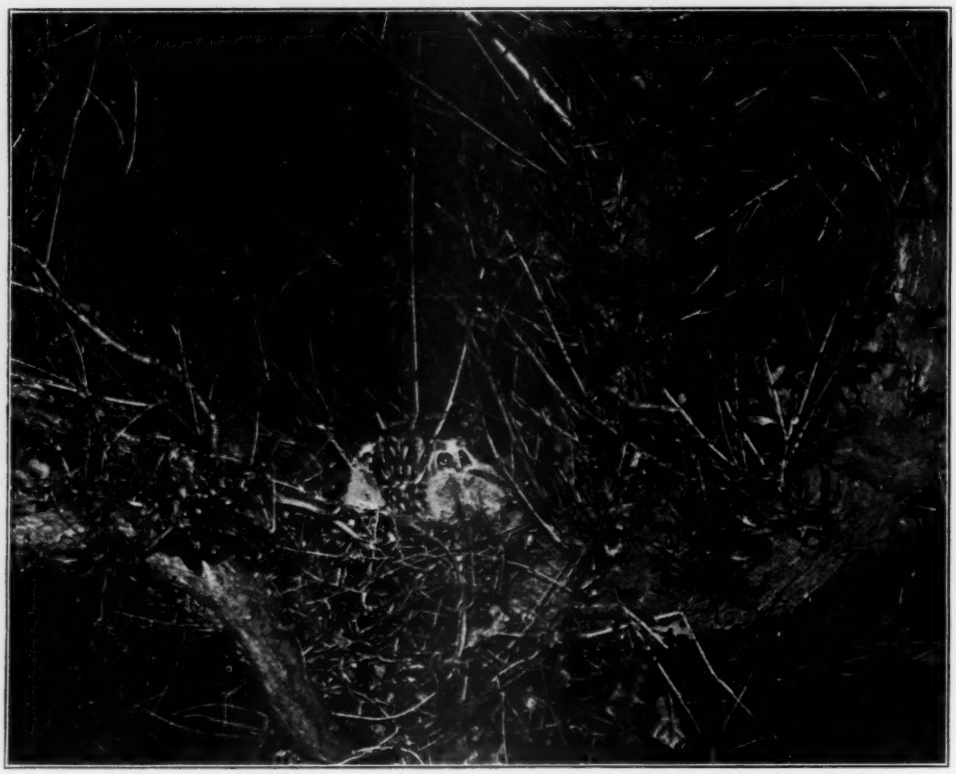
TABELLE 21. *Der Wacholderdrosselngehalt der Waldohreulen- bezw. Sperbernahrung während der Wacholderdrosselninvasion (vgl. D 2. Seite 520) im Vergleich mit dem mittleren Wacholderdrosselngehalt.*

	Während "Invasion"	Im Durchschnitt
Wacholderdrossel v. Eule	7 (22)	10 (3279)*
Wacholderdrossel v. Sperber	14 (70)	39 (832)

* Ausser diesen 10 Wacholderdrosseln haben wir für die Eule möglich noch mehrere zu rechnen, weil sich unter den 149 Drosseln spec. (siehe Tabelle 1), die zwar hauptsächlich Amseln vergegenwärtigen (Rupfungen!), noch einige Wacholderdrosseln befinden können. Nehmen wir jedoch an, alle 149 Drosseln spec. wären Wacholderdrosseln, so bleibt die Tabelle 21 doch noch überzeugend!

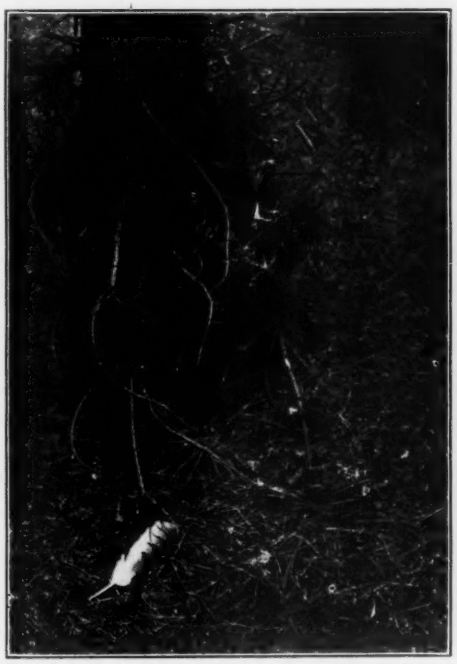


Waldohreule mit Feldmaus in dem linken Fang auf dem Horst. Aufnahme mit Hauff Vacu-Blitz von N. Tinbergen.

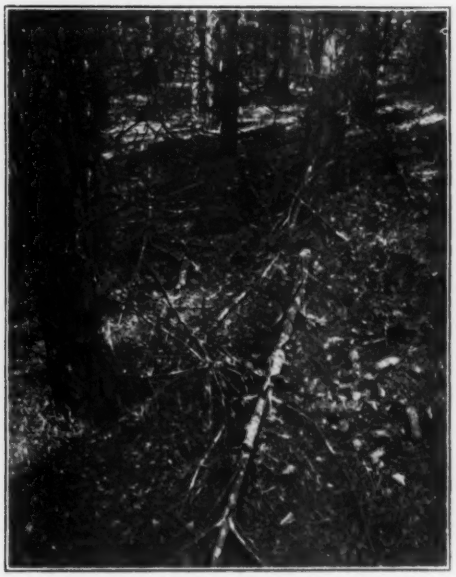


Waldohreule mit 2 fast flüggen Jungen auf dem Horst. Aufnahme mit Hauff Vacu-Blitz von F. P. J. Kooymans.

Karakteristische Überwinterungsstelle einer Trupp Waldohreulen.
Aufnahme N. Tinbergen.

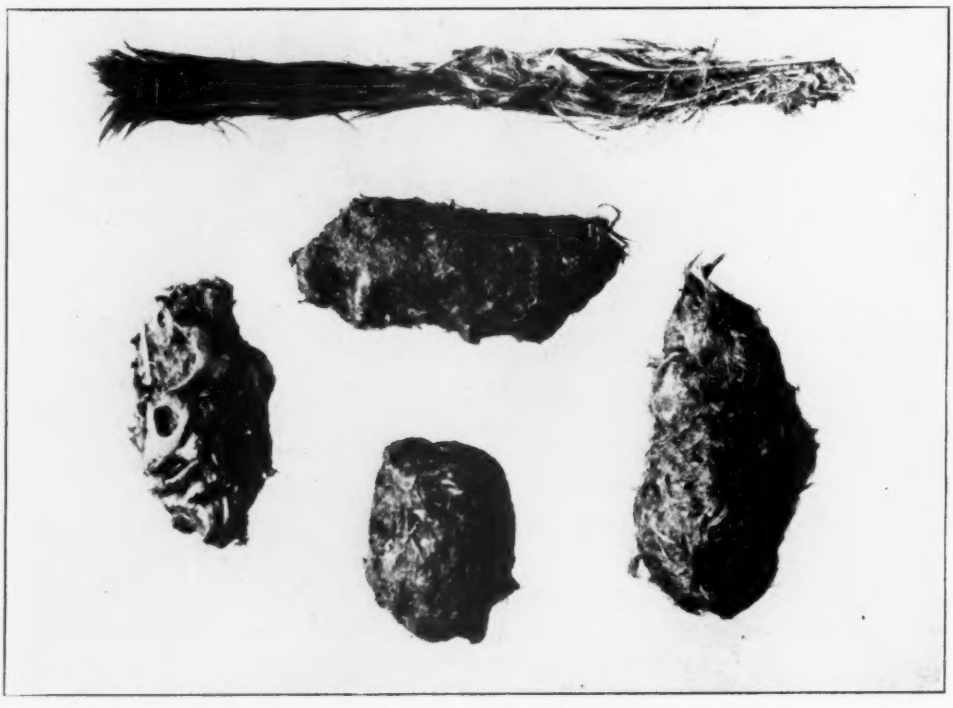


Ruhebaum einer Waldohreule im Sommer: einige wenige Gewölle, wenig Geschmeiss, frisch vermauserte Schwinge. Aufnahme N. Tinbergen.

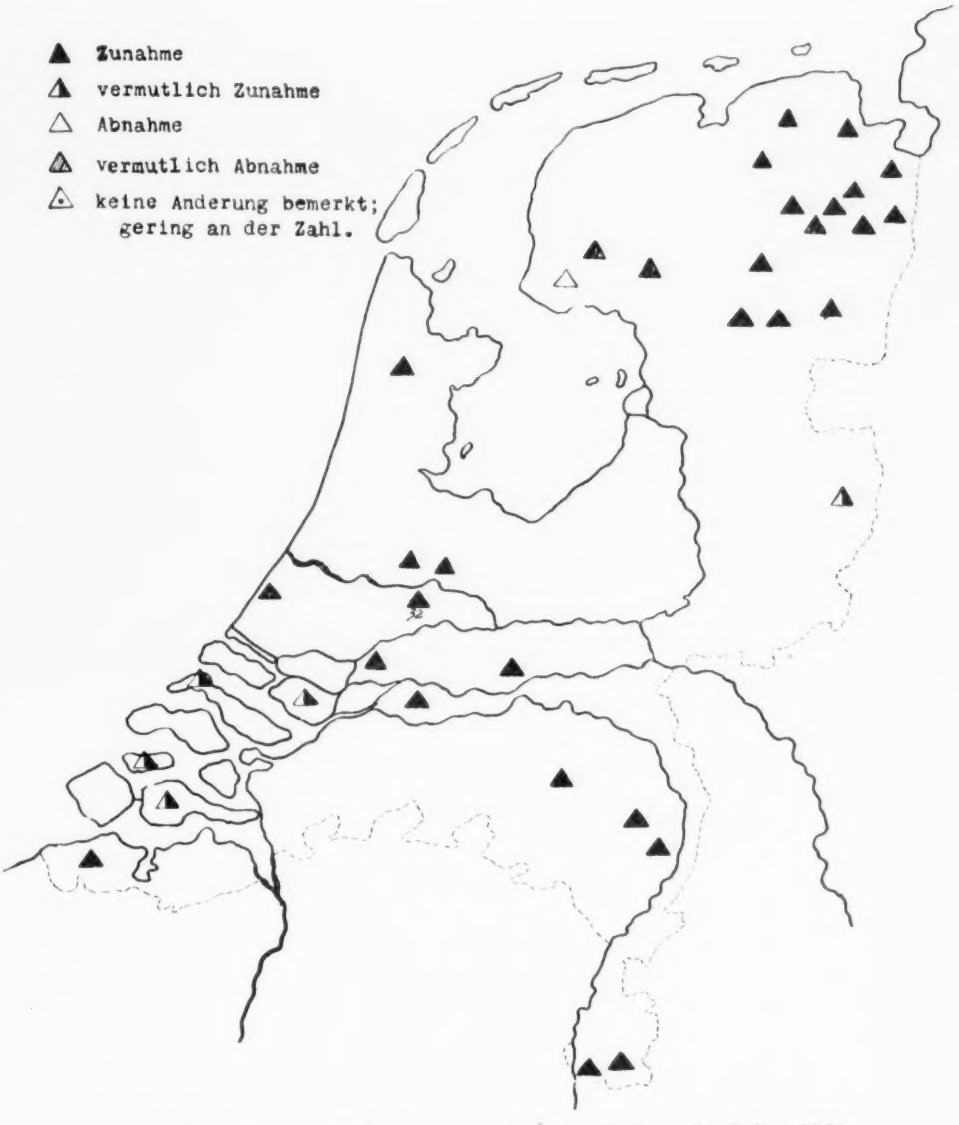


Von mehreren Waldohreulen benutzter Ruhebaum im Winter: viele Gewölle, Grund weiss gekalkt. Aufnahme G. J. Broekhuysen.

Karakteristische, von der Waldohreule herrührende Baumrupfung eines Buchfinken. Aufnahme N. Tinbergen.



Waldohreulengewölle mit Vogelresten (Drosselschwanz, Spatzenschnabel) und Mäuseresten. Aufnahme N. Tinbergen.



Änderungen in dem Feldmäusebestand in Holland im Jahre 1930.

Änderungen in dem Feldmäusebestand in Holland im Jahre 1931. Für die Erklärung der Dreiecke siehe vorige Abbildung